

A NEW GENUS OF AMORBINI (HETEROPTERA: COREIDAE) FROM AUSTRALIA, WITH TWO NEW SPECIES

H. BRAILOVSKY AND G.B. MONTEITH

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A new genus (*Kurrajongia*) containing two new species (*K. armata* and *K. aploa*) in the tribe Amorbin (Coreidae) is described. Both species feed on *Brachychiton* spp. (Sterculiaceae) in eastern Australia. Dorsal view illustrations of adults and nymphs and drawings of the male and female genitalia are provided, as well as a key and biological notes. □ Hemiptera, Coreidae, Amorbin, Brachychiton.

H. Brailovsky, Instituto de Biología UNAM, Departamento de Zoología, Apartado Postal #70153, Mexico 04510 D.F.; G.B. Monteith, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 1 October, 1997.

The tribe Amorbin (Hemiptera: Heteroptera: Coreidae) has 6 described genera in the Australian region: *Acroelytron* Mayr (1 species), *Amorbus* Dallas (15 species), *Cheius* Stål (1 species), *Gelonus* Stål (1 species), *Kurnaina* Distant (1 species), and *Tambourina* Distant (1 species).

This paper describes a new genus of Amorbin with two new species, both of which are associated with the common Kurrajong trees (*Brachychiton populneus* and *B. diversifolius*) in eastern Australia. They are moderately large (15-20mm) bugs with a speckled greyish appearance which occur in large clusters on the trunks of the trees. However, due to their camouflaged appearance they have been virtually overlooked by collectors until recent years when their host tree became known.

The following abbreviations are used for institutions where specimens are located: ANIC = Australian National Insect Collection, Canberra; AM = Australian Museum, Sydney; DPIQ = Department of Primary Industries, Indooroopilly, Brisbane; IBUNAM = Instituto de Biología (Colección Entomológica), Universidad Nacional Autónoma de México, Mexico City; QM = Queensland Museum, Brisbane; SAM = South Australian Museum, Adelaide; UQIC = University of Queensland Insect Collection, Brisbane. Abbreviations used in the label data lists: GBM = G.B. Monteith; SF = State Forest; NP = National Park. All measurements are given in mm.

Kurrajongia gen. nov.

ETYMOLOGY. For the common name of Kurrajong given to the host trees of both species included in the genus. Kurrajongs are familiar trees of inland eastern Australia.

TYPE SPECIES. *Kurrajongia armata* sp. nov. (Fig. 1).

DIAGNOSIS. The new genus resembles *Gelonus* Stål in having head and pronotum wider than long, tylus unarmed and extending anteriorly to the jugae, tibiae sulcate, and the abdominal sternite VII of the ♀ with plica and fissura. It also lacks the incrassate hind femora which are found in *Amorbus* but not in *Gelonus* (Steinbauer, 1995).

In *Kurrajongia* the rostrum reaches the metasternum, with rostral segment III longer than 1.30mm. The apex of the tylus reaches or extends beyond the antenniferous tubercles, the femora are unarmed, the eyes are large, slightly stylate and project beyond the lateral margins of the head. The pronotal calli are elevated and irregularly rounded at each side. In *Gelonus* the rostrum is shorter, reaching only on to the anterior part of the mesosternum, with rostral segment III shorter than 0.60mm. The tylus is short extending slightly beyond the antenniferous tubercles and the femora are armed. The eyes are hemispherical and not conspicuously projecting, with the calli almost flat.

DESCRIPTION. *Head*. Width across eyes greater than length, non declivent, pentagonal, produced beyond antenniferous tubercles and dorsally flat; tylus laterally compressed and projecting upward as an acute projection; jugae unarmed, apically subglobose and shorter than tylus; antenniferous tubercles prominent, obliquely truncate, unarmed; antennal segment I robust, thickest, slightly curved outwards and longer than head; segments II and III terete and robust; segment IV fusiform; antennal segment II the longest, segment III the shortest; ocelli raised on low tubercles; preocellar pits deep; postocellar pits deep or slightly excavated; eyes large,

slightly stylate, hemispherical, projecting conspicuously beyond lateral margins of the head; postocular tubercle relatively small; bucculae elongate, angulate anteriorly, not extending beyond middle third of eyes, with external edge sinuate or entirely rounded; rostrum at least to anterior edge of metasternum and sometimes a little further; rostral segments I and IV subequal, segments II and III subequal and slightly shorter than I and IV; mandibular plate absent; frons with deep central longitudinal incision.

Thorax. Pronotum trapeziform, clearly or slightly wider than long, moderately declivent; collar wide; frontal angles produced forward as medium to broad, short projections; anterior margin entire; anterolateral margins almost straight or slightly concave, with short and subacute spines or nodules; humeral angles rounded or acute and produced into a short, laterally directed, conical tooth; posterolateral edge straight or sinuate; posterior edge straight; callus elevated, irregularly rounded at each side, divided along midline by a longitudinal furrow and ending on a deep almost circular central depression; disc striate and densely tuberculate. Anterior lobe of metathoracic peritreme elevated and auriculiform, posterior lobe sharp, small; propleura, mesopleura, and metapleura densely tuberculate; mesosternum with median sulcus, flanked by two elevated ridges.

Legs. Fore coxal cavities slightly opened, middle cavity wide and conspicuously opened, and hind cavity open; femora unarmed, densely tuberculate; tibiae terete, sulcate.

Scutellum. Triangular, length equal to or slightly greater than width; anterior third elevated, with anterior margin and posterior third flat; apex subacute; disc and apex densely tuberculate; anterior margin and anterolateral areas striate and polished black.

Hemelytra. Macropterous, almost reaching the apex of the last abdominal segment; costal margin emarginate; apical margin clearly sinuate with inner third concave and outer third straight; apical angle obtuse; hemelytral membrane elongate with several longitudinal veins, few of them bifurcate.

Abdomen. Connexival segments reflexed above margin of hemelytron at rest; posterior angles of connexival segments simple, not spinose; abdominal sterna with weak medial depression, extending to middle third of sternite V.

Female genitalia. Abdominal sternite VII with plica and fissura; plica narrow, rectangular, with

outer margin straight to slightly concave; gonocoxae I conspicuously enlarged dorso-ventrally, larger than paratergite IX, in caudal view closed, in lateral view slightly convex; paratergite VIII triangular, with spiracle visible; paratergite IX square, larger than paratergite VIII. Spermatheca: Fig. 2A.

Male genitalia. Genital capsule: Posteroventral margin emarginate (Fig. 2B, E), with edge rounded and slightly excavated on the midline. Parameres: Inner margin of the basal portion of the body with a lobe projecting anteriorly; inner margin of the middle third of the body flattened, extending anteriorly, and sometimes reaching the basal lobe; distal portion hook-like (Fig. 2C-D, F-G).

Integument. Body surface rather dull, with long or short, decumbent to suberect, golden or silvery, bristle-like hairs. Head, pronotum, scutellum, clavus, corium, connexival segments, thorax, femora, tibiae, and abdominal sterna densely tuberculate; pronotum and scutellum irregularly striate.

KEY TO SPECIES OF *KURRAJONGIA* GEN. NOV.

1. Humeral angles of the pronotum produced into an angulate tooth; pronotum clearly wider than long; second antennal segment with an apical, white ring; third antennal segment with no more than apical half pale; basal two segments of hind tarsus white, contrasting with very dark apical segment; parameres as in Fig. 2F-G

..... *K. armata* sp. nov.

- Humeral angles of the pronotum rounded; pronotum with length about equalling width; second antennal segment without white apex; third antennal segment with more than apical half pale; basal two segments of hind tarsus not contrastingly pale; parameres as in Fig. 2C-D.

..... *K. aploa* sp. nov.

Kurrajongia armata sp. nov. (Figs 1, 2E-G, 4A, 6)

ETYMOLOGY. Named for the angular projections of the humeral angles of pronotum.

MATERIAL. HOLOTYPE: QMT46015 ♂, Braemar SF via Kogan (Qld), 15-19.x.1979, G.B. Monteith, in QM. **PARATYPES** (nymphs (N) listed are not types) (Qld): 2 ♀, same data as holotype, in QM; 4 ♂ 3 ♀, same locality, 4.iv.1996, on *B. populneum*, GBM, in QM; 1 ♀, 40km S of The Lynd, 13.ix.1982, GBM, in IBUNAM; 12 ♂ 9 ♀ 5 N, Burnett R., 3km W Eidsvold, 14.iv.1996, on *B. populneum*, GBM, in QM; 39 ♂ 30 ♀ IN, Mt Moffatt NP, Rotary Shelter Shed, 27.ii.1996, on *B. populneum*, GBM, in QM, ANIC, SAM; 2 ♀, Mt Moffatt NP, Kenniff's Lookout,

13.xii.1987, GBM, Thompson & Yeates, in IBUNAM & UQIC; 3 ♀ ♀ 1N, Mt Moffatt NP, Mt Rugged Summit, 27.ii.1996, on *B. populneum trilobus*, GBM & C.J. Burwell, in QM; 1 ♂ 1 ♀ 2N, Cracow, 13.iv.1996, on *B. populneum*, GBM, in QM; 1 ♀, 34km N of Taroomb, 20.ix.1997, GBM, on *B. populneum*, in QM; 4 ♂ ♂ 1 ♀, 'The Amphitheatre', Expedition Ra NP, 24-26.ix.1997, D. & L. Cook, on *B. populneum trilobus*; 1 ♂ 1 ♀ 3N, 25km N Monto, 10.iv.1996, on *B. populneum*, GBM, in QM; 6 ♂ ♂ 1 ♀ 1N, Binjour Plateau, via Gayndah, 14.iv.1996, on *B. populneum*, GBM, in QM; 1 ♂, 50km W Eidsvold, 14.iv.1996, on *B. populneum*, GBM, in QM; 1 ♀, 5km S Bogantungan, 12.iv.1996, on *B. populneum*, GBM, in QM; 2N, Auburn River NP, via Mundubbera, 17-19.iv.1987, on *B. populneum*, GBM, in QM; 3 ♂ ♂ 1N, 2ml WNW Beta, 30.iv.1957, Key & Chinnick, in ANIC; 2 ♂ ♂ 1 ♀, Chinchilla, 14.xi.1988, D. Bunting, in DPIQ and IBUNAM; 1 ♀, 'Allinga', Chinchilla, 17.v.1984, G. Lithgow, in QM; 1 ♀, Chinchilla town, 16.ii.1984, G. Lithgow, in QM. (QM Paratypes: QMT46016-46049, 46051-46074, 46076-46128, 46133-46138).

DIAGNOSIS. *Kurrajongia armata* is easily distinguished from the only other species in the genus by its shorter, broader form and the characters given in the key. The parameres (Fig. 2F-G) are also distinct.

DESCRIPTION. MALE. Colouration. Dorsal: pale orange yellow with tubercles orange hazel; following areas black to dark red brown: sides of head in front of eyes, ocellar tubercle, two longitudinal bands running laterad of midline on the anterior and middle third of pronotal disc, two large spots on the posterior margin of pronotal disc, basal angle, anterior margin (except midline) and lateral margins of the anterior third of scutellum, irregular spots scattered on clavus and corium, and a square spot on the midline of connexival segments III to VII; apex of scutellum pale yellow; hemelytral membrane dirty ambarine, with veins, basal angle and some discoidal or irregular spotting dark brown; abdominal segments bright orange yellow, with most of VII black; antennal segments I and II with ventral side black, and dorsal side red brown with irregular spotting yellow; apical one tenth of II yellow; segment III with basal three fifths black, and distal two fifths yellow; segment IV dark red brown with basal yellow ring. Ventral: Pale orange yellow with tubercles bright red brown to bright orange hazel; following areas black: apex of rostral segment IV, area around the metathoracic peritreme, anterolateral margins and spines of the thoracic pleura, most of mesosternum, scattered spots on abdominal sterna III to VII, and genital capsule and middle third of pleural sterna III to



FIG. 1. Dorsal view of ♀ *Kurrajongia armata*.

VII; coxae hazel brown with external margin pale yellow; trochanters pale yellow with some ventral hazel brown spots; femur pale yellow with tubercles red brown, and two black irregular rings, one subbasal, the other subdistal; tibiae pale yellow, densely marked with red brown tubercles, with base and apex mostly black; hind tarsus segments I and II pale yellow and segment III dark hazel orange; anterior and posterior lobes of metathoracic peritreme, the area around each abdominal spiracle, and one or two discoidal or irregular spots on prothorax, mesothorax, and metathorax pale yellow to creamy yellow.

Structure. Pronotum: Clearly wider than long; frontal angles produced forward as medium-sized projections; anterolateral margins emarginate, obliquely straight or slightly concave, with short and subacute spines; humeral angles acute, produced into laterally-directed, conical teeth; posterolateral edge sinuate.

Genital capsule. Posteroventral margin emarginate, with edge rounded, and slightly excavated on the midline (Fig. 2E). Parameres: Fig. 2F-G.

FEMALE. Colouration. Similar to ♂. Connexival segments VIII and IX black or red brown with

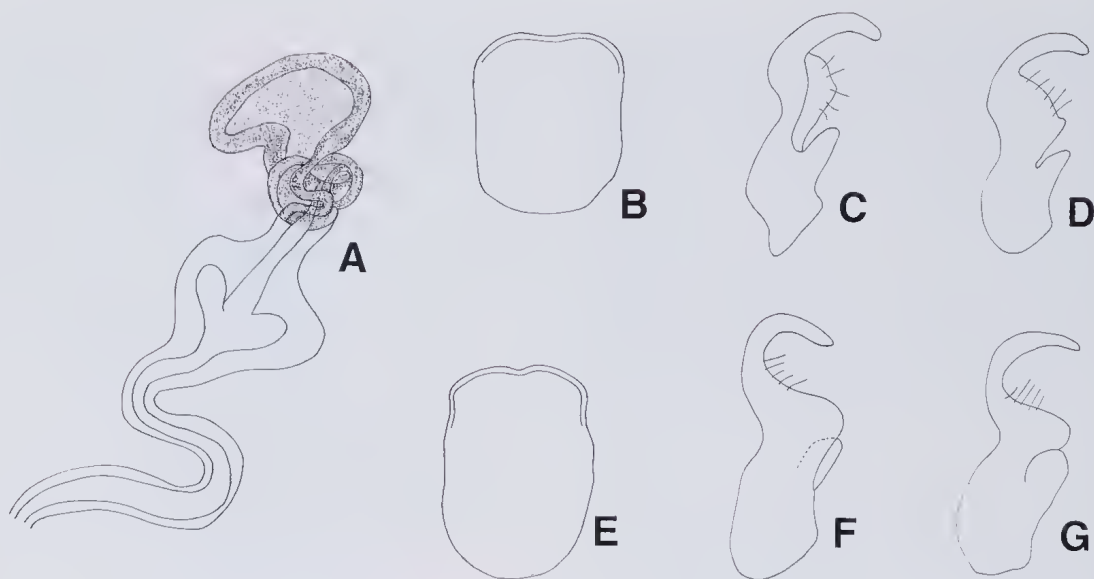


FIG. 2. A-D, *Kurrajongia aploa*; A, ♀ spermatheca; B, ♂ genital capsule; C-D, ♂ parameres. E-G, *Kurrajongia armata*; E, ♂ genital capsule; F-G, ♂ parameres.

posterior third orange yellow; dorsal segments VIII and IX black, with following areas dark orange yellow; longitudinal midline band, and lateral edges; genital plates pale orange yellow, with tubercles, and each edge of paratergite VIII and IX black to red brown. Variation: 1, femora pale yellow, with tubercles and irregular spots red brown, and with only one black subdistal ring; 2, abdominal sternite VII with fissura mostly black. *Measurements* (mm). ♂ first, then ♀. Head length: 1.80, 2.10; head width across eyes: 2.40, 2.62; interocular space: 1.35, 1.50; interocellar space: 0.47, 0.52; length antennal segments: I, 3.30, 3.40; II, 3.85, 3.95; III, 2.65, 2.80; IV, 3.40, 3.40; length rostral segments: I, 1.30, 1.60; II, 1.20, 1.30; III, 1.20, 1.40; IV, 1.40, 1.55. Pronotum: Total length: 3.10, 3.55; width across humeral angles: 2.05, 2.30; width across humeral angles: 4.35, 5.40. Scutellar length: 1.85, 2.20; width: 1.75, 2.20. Total body length: 14.00, 16.90.

DISTRIBUTION (Fig. 5). Widely distributed in central western Queensland from a little west of the Darling Downs, north almost 1200km to near The Lynd, SW of the Atherton Tableland. A sighting record by the second author is available for nymphs on Kurrajong trees at Granite Gorge, just W of Mareeba. This would extend the known range of the species another 250km further north but requires adults for confirmation.

***Kurrajongia aploa* sp. nov.**
(Figs 2A-D, 3, 4B)

ETYMOLOGY. From *aploos* (Greek adjective meaning simple), refers to the lack of spines on the humeral angles of the pronotum.

MATERIAL. HOLOTYPE: QMT46014 ♂, Maidenwell (Qld), 18.iii.1996, on *Brachychiton populneus*, GBM, in QM. PARATYPES (nymphs listed are not types) (Qld): 2 ♀ 1N, same data as holotype, in QM; 1 ♂ 2 ♀, Bluff R. foothills, via Biggenden, 1-7.i.1972, H. Frauca, in ANIC; 2 ♀ 1N, Cooyar, 18.iii.1996, on *B. populneus*, GBM, in QM, SAM; 2 ♂ 3 ♀ 4N, Mistake Mtns via Cunninghams Gap, 10-12.iii.1978, 1000-1100m, on *B. populneus*, GBM and D. Booth, 1 ♂ 2 ♀ 4N in UQIC and 1 ♂ 1 ♀ in IBUNAM; 1 ♂ 1 ♀, Gayndah, Masters, in AM; 1 ♀, no data., in DPIQ; 1 ♂, Brisbane, 4.x.1925, in IBUNAM; 1 ♀, Brisbane, 6.iii.1960, C.J. Paul, in QM; 1 ♂ 1 ♀, no data, in AM; 1N, Nundubbermere Falls, 25km SW Stanthorpe, 2-3.iv.1988, on *B. populneus*, GBM, in QM; 1 ♂, 6km N of Taroom, 2.iii.1991, G. Daniels, in UQIC; New South Wales: 6 ♂ 3 ♀ 22km W of retreat (35km E of Manilla, 600m, 23.x.1995, Schuh & Cassis, in AM and QM; 1 ♂, Tenterfield, 3.i.1942, R. Pullen, in AM. (QM Paratypes: QMT46050, 46075, 46129-46132).

DIAGNOSIS. *Kurrajongia aploa* can be recognized by its more elongate form, the humeral angles which are rounded and not produced, and characters of the antennae and hind tarsi given in the key. The parameres (Fig. 2C-D) are also distinct.

DESCRIPTION. MALE. Colouration. Dorsal: Pale orange yellow with tubercles orange hazel; following areas black to dark red: sides of head in front of eyes, ocellar tubercle, preocellar pits, postocellar pits, lateral margins of vertex, two longitudinal bands running laterad of midline of the anterior and middle third of pronotal disc, basal angle, anterior margin (except midline), and lateral margin of the anterior third of scutellum, and irregular spots on clavus and corium; pronotal disc scattered with some creamy yellow spots; hemelytral membrane dirty ambarine, with veins, basal angle, and some discoidal or irregular spots dark brown; apex of scutellum yellow; connexival segments black with anterior angle and posterior margin yellow; abdominal segments bright orange yellow, with the greatest part of VII and lateral portion of VI black; antennal segments I and II, with ventral side black and dorsal side red brown with yellow marks; segment III yellow with basal third black; segment IV black to red brown, with narrow basal ring yellow. Ventral: Pale orange yellow with tubercles bright red brown to bright orange hazel; following areas black: apex of rostral segment IV, area around lobes of the metathoracic peritreme, anterolateral margins of the thoracic pleura, four discoidal spots on the anterior margin of abdominal sternite IV, and two on the sterna V and VI, and one row of discoidal spots near abdominal spiracles of sterna III to VII; anterior and posterior lobe of metathoracic peritreme, the area around each abdominal spiracle, and some discoidal or irregular spots on prothorax, mesothorax, and thoracic metapleura pale to creamy yellow; coxae and trochanters pale yellow, with some dark brown spots; femora dirty yellow, with tubercles and marks red brown, and with subdistal irregular black ring; tibiae dirty yellow, and densely covered by dark red brown spots; hind tarsal segments I and II hazel orange; segment III dark hazel orange.

Structure. Pronotum slightly wider than long; frontal angles produced forward as broad projection; anterolateral margins emarginate, almost straight, and nodulose; humeral angles rounded; posterolateral edge almost straight.

Genital capsule. Posteroventral margin conspicuously emarginate, protruding, with edge rounded, and slightly excavated on the midline (Fig. 2B). Parameres: Fig. 2C-D.

FEMALE. Colouration; Similar to ♂. Connexival segments VIII and IX black to red brown; dorsal segments VIII and IX black, with following areas dirty orange yellow: longitudinal band

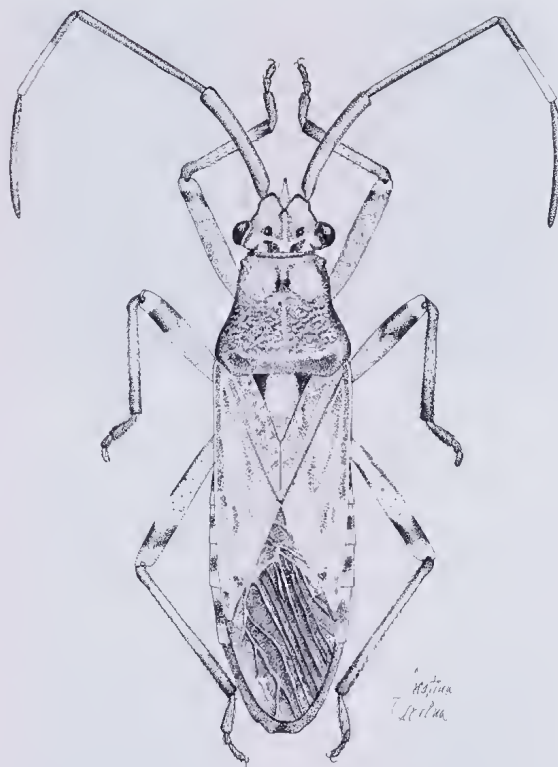


FIG. 3. Dorsal view of ♂ *Kurrajongia aploa*.

at midline of segment IX, and lateral portions of each segment; genital plates pale orange yellow, with basal angle of gonocoxae I, external edge of paratergite IX, and small spot near the spiracle of paratergite VIII black.

Measurements (mm). ♂ first, then ♀. Head length: 2.25, 2.55; width across eyes: 3.15, 3.25; interocular space: 1.75, 1.92; interocellar space: 0.57, 0.57; length antennal segments: I, 3.50, 3.85; II, 4.60, 4.85; III, 2.85, 3.20; IV, 3.40, 3.63; length rostral segments: I, 1.70, 2.00; II, 1.50, 1.75; III, 1.40, 1.65; IV, 1.70, 1.90. Pronotum: total length: 3.75, 4.50; width across frontal angles: 2.35, 2.70; width across humeral angles: 3.90, 5.00. Scutellar length: 2.00, 2.30; width: 1.70, 2.00. Total body length: 17.10, 20.40.

DISTRIBUTION (Fig. 5). This species is known from a series of localities, mostly at higher altitude, along the Dividing Range from Tenterfield in far northern New South Wales north to the Cooyar-Maidenwell district just north of Toowoomba in southern Queensland. Beyond that area there is one record 150km further north at lower elevations on the subcoastal ranges near Biggenden and another from 200km to the west

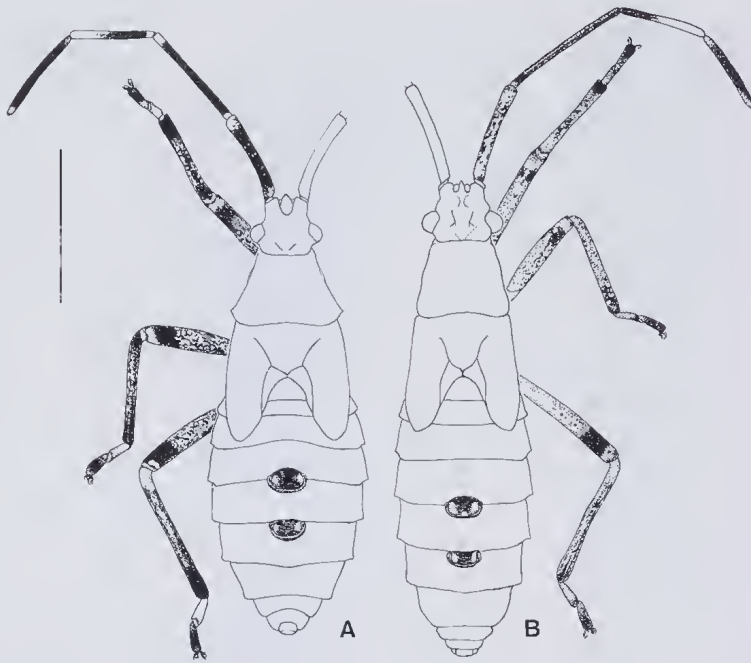


FIG. 4. Last instar nymphs of *Kurrajongia* spp. A, *K. armata*. B, *K. aploa*.

near Taroom. There are two early records from Brisbane which have not been repeated by recent collecting. Except for the Taroom locality the distribution of *K. aploa* is allopatric with respect to that of *K. armata* which is generally further inland.

HOST PLANTS OF KURRAJONGIA SPECIES

All host records for these bugs are from trees of *Brachychiton* Schott & Endl. (Sterculiaceae) which has been recently monographed by Guymer (1988). It includes trees commonly known as Bottle Trees and Kurrajongs. *Brachychiton* is considered to be one of the older endemic components of the Australian flora and has 31 species of which 30 occur in Australia and 2 in New Guinea. Within Australia they occur across the north and east of the continent with one species in the central deserts. Centres of diversity are in the Kimberley (9 spp) and in Cape York Peninsula (10 spp). However records of *Kurrajongia* are all from only two of the three non-deciduous species which form the Section *Poecilodermis* of *Brachychiton*. These are the familiar trees known as Kurrajongs and which are widely retained (or replanted) on farms in eastern Australia because of their value as drought relief fodder for stock. The species are the common Kurrajong, *B. populneus* (Schott & Endl.) R.Br. in Horsfield, and the northern Kurrajong, *B. di-*

versifolius R.Br. in Horsfield. Their distribution in eastern Australia and the records for *Kurrajongia* species are shown in Fig. 5. *B. populneus* is divided into two subspecies and the dotted line shows the approximate boundary between them based on information in Guymer (1988) and more recent herbarium records provided by that author. Almost all records for both species of *Kurrajongia* are from *B. populneus* but the two records from north Queensland (*K. armata* at The Lynd; presumed nymph of *K. armata* from Granite Gorge) are from within the range of the closely related *B. diversifolius*. In the south the two subspecies of *B. populneus* were not all differentiated at the time of collection of the bugs. However it appears that all records of *K.*

aploa are from *B. populneus populneus* while *K. armata* occurs on both that subspecies and on *B. p. trilobus* Guymer. The single Taroom specimen of *K. aploa* is puzzling because there appears to be no Kurrajong trees at the locality. When the locality was revisited in Sept., 1997 the only *Brachychiton* found was the narrow leafed bottle tree, *Brachychiton rupestris* (Mitchell ex Lindley) Schumann but *Kurrajongia* was not found on that tree.

Although there is a diverse flora of *Brachychiton* species available in Australia, it is very curious that the two very distinct species of *Kurrajongia* which have arisen both feed on a very small taxonomic range of species. This may be an artefact of collecting because these bugs are very cryptic and require special search. However within the region of southern Queensland where the bugs are common on *B. populneus* there are at least five other *Brachychiton* species which have been examined by the second author without results. *Brachychiton* species in other areas may repay attention.

BIOLOGY OF KURRAJONGIA SPECIES

Both species are found on the trunks of the trees where they adopt a flattened posture against the rough bark which makes them very hard to see. A characteristic habit of both species, at least in late summer, is the formation of very large aggrega-

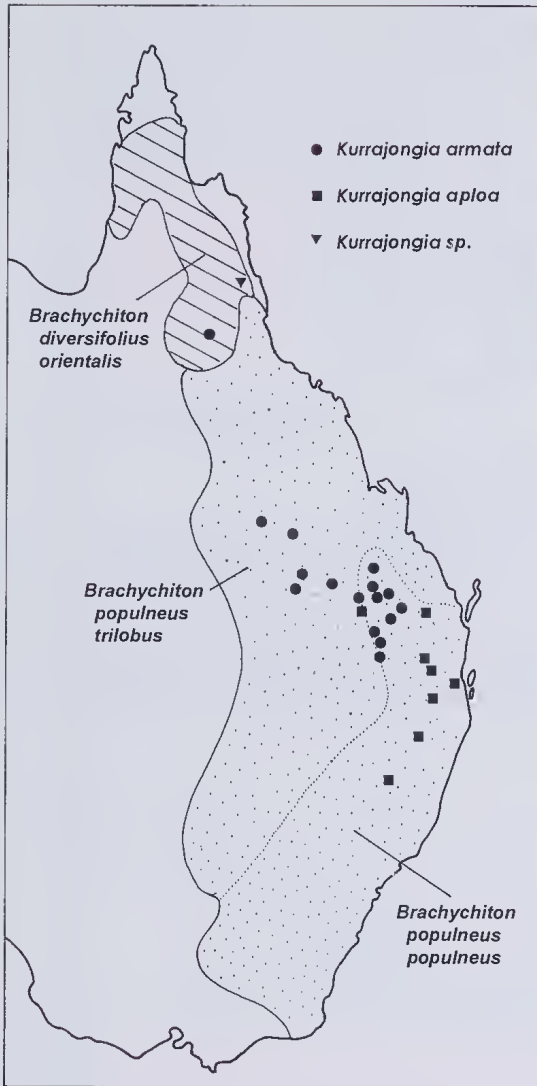


FIG. 5. Distribution map of *Kurrajongia* spp. and their *Brachychiton* food plants in eastern Australia.

tions of mixed adults and nymphs. These may number several hundred individuals and may measure 20cm in diameter. These aggregations form a quiescent patch on the trunk, often at about the level of the lower limbs of the tree. When disturbed they move en masse around the trunk and settle again. If disturbed vigorously they synchronously discharge their scent glands which provides a formidable group defence. *Kurrajongia armata* has only been taken on the main trunks of the trees but *K. aploa* individuals are occasionally found on the smaller branches and



FIG. 6. Living adult ♀ of *Kurrajongia armata* on foliage of *Brachychiton populneus*.

twigs where they adopt the same flattened posture lengthways on the twigs.

Egg laying has not been observed though a single old egg, presumed to be of *K. armata*, was found in a bark crevice adjacent to an aggregation of that species.

The nymphs are similarly coloured to the adults and have no aposematic colour or behaviour as seen, for example, in *Amorbus* nymphs. Last instars of both species are shown in Fig. 4. They can be separated by the same prothorax, antenna and tarsal features described in the key to adults.

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EASTERN RANGE EXTENSION OF FORREST'S MOUSE (*LEGGADINA FORRESTI*). *Memoirs of the Queensland Museum* 42(2): 386. 1998:- Forrest's Mouse (*Leggadina forresti*) is generally restricted to arid inland areas of Australia (Reid & Morton, 1995; Watts & Aslin, 1981). Specimen records from the Queensland Museum mammal database indicate that the eastern-most registration of *L. forresti* is from 'Hillgrove' (19°38'S 145°43'E). Regurgitated owl pellets collected from Mt Castor (23°30'25"S 147°01'51"E), Gemini NP in central Qld during 1995 extended the eastern range of the species by approximately 210km. Here, we report the capture of two specimens of *L. forresti* from properties near Rolleston (24°28'00"S 148°37'30"E), approximately 250km SE of Mt Castor and 300km E of 'Hillgrove', where previous records of the species have been collected.

During April, 1997 fauna surveys were completed in the forests and woodlands surrounding Rolleston, central Queensland. Two specimens of *L. forresti* were captured in two separate tracts of open forest, dominated by *Eucalyptus coolabah*. Both specimens were captured in pitfall traps that consisted of three, 20-litre buckets, spaced 5m apart, set so that the lip of each bucket was flush with the ground. A 20m-long drift fence was erected dissecting the mouth of each bucket. A total of 96 pitfall trap-nights were undertaken during the fauna survey of the area.

One ♂ *L. forresti* was captured on 'Sirius' (24°25'25"S 148°36'30"E) and one ♀ (QMJM11585) approximately 6.5km to the SE on 'Hillview' (24°28'40"S 148°38'10"E). Both areas were of riparian vegetation along Comet R. The soils at the sites were cracking clay alluvials. Other mammals

recorded during the survey mostly reflect eastern assemblages. They included: *Planigale ingrami* (coolibah forest, 'Venus Downs'); *Macropus parryi* (edge of grassland and coolibah forest, 'Venus Downs'); *Melomys burtoni* (semi-deciduous vine forest, 'The Lake'); *Canis lupus dingo* (grassland, 'The Lake'); *Sminthopsis macroura* and *S. murina* (coolibah forest, 'Hillview'); *Pseudomys delicatulus* (silver-leaved ironbark woodland, 'The Crescent'); *Chalinolobus picatus* and *C. nigrogriseus* (creek in brigalow forest, 'The Crescent'); *Mus musculus*, *Nyctophilus geoffroyi*, *N. gouldi*, *Scotorepens greyii*, *Saccolaimus flaviventris*, *Mormopterus beccarii*, *Nyctinomus australis*, *Macropus giganteus* and *Trichosurus vulpecula* (throughout study area); *Petauroides volans* (riparian zone along the Comet R., 'The Lake'); *Tachyglossus aculeatus* (coolibah forest, 'Blockadirt').

Acknowledgements

We thank Mr Ivan Eyles ('Hillview') and Mr Des Priddle ('Sirius') for allowing access onto their properties during the survey. Data records were supplied by H. Janetzki, Queensland Museum.

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PONTONIINE SHRIMPS FROM MORETON BAY, QUEENSLAND (CRUSTACEA:
DECAPODA: PONTONIINAE)

A.J. BRUCE

Bruce, A.J. 1998 06 29: Pontoniine shrimps from Moreton Bay, Queensland (Crustacea: Decapoda: Pontoniinae). *Memoirs of the Queensland Museum* 42(2): 387-398. Brisbane. ISSN 0079-8835.

Three recently collected new species of pontoniine shrimps from Moreton Bay, southern Queensland, are described and illustrated. *Periclimenes terangeri* was associated with an unidentified actinarian, while the hosts of *Onycocaris stradbrokei* and *Periclimenaeus myora*, probably a sponge and a tunicate respectively, were not identified. These additional species increase the pontoniine fauna known from Moreton Bay to about 20 species. □
Natantia, Pontoniinae, new species, Moreton Bay, Queensland.

A.J. Bruce, Crustacea Section, Queensland Museum, P.O. Box 3300, South Brisbane 4101, Australia; 4 July, 1997.

The pontoniine shrimp fauna of Moreton Bay, Queensland (Qld), is of particular interest as it is nearing the southern limit of the Indo-West Pacific zoogeographical region. The first species recorded, *Coralliocaris graminea*, *C. superba*, *Jocaste lucina*, *Periclimenes amymone* and *P. madreporae* (as *P. inornatus*), all associates of branching corals from Myora, were reported by Patton (1966). Since then a further 13 species only have been recorded in published literature, making a total of 20 species. This is in marked contrast with the fauna of Heron I., at the southern end of the Great Barrier Reef, some 480 km to the north, where the pontoniine fauna has received more intensive study and well over 100 species are known to occur. The discovery of three new species in Moreton Bay suggests that still further species may be expected to be present. A new species of *Pontonia* was also collected and will be described elsewhere. The type specimens are deposited in the collections of the Queensland Museum.

In the descriptions, carapace length refers to the postorbital carapace length (POCL).

SYSTEMATICS

Class CRUSTACEA

Order DECAPODA Latreille, 1803

Family PALAEMONIDAE Rafinesque, 1815

Sub-family PONTONIINAE Kingsley, 1878

Periclimenes terangeri sp. nov.

(Fig. 1)

ETYMOLOGY. Aboriginal, *terangeri*, Stradbroke Island.

MATERIAL. HOLOTYPE: QMW21735, 1 ovig. ♀; Polka Point, North Stradbroke I. Qld, 27°30'S

153°23'E, 0.5 m, coll. P. Davie and J. Short, 6 March 1996, in sea-grass. PARATYPE: QMW22275, 1 ovig. ♀ (dissected), same collection data as holotype.

DESCRIPTION. A small, slender *Periclimenes* species, of subcylindrical body form, generally similar to *P. toloensis* Bruce.

Adult female. Rostrum (Fig. 1A) slender, straight, slightly up-turned, c. $1.15 \times$ carapace length, slender, acuminate, reaching to slightly beyond end of antennular peduncle, with 9 acute evenly spaced dorsal teeth, 1st tooth epigastric, 2nd situated posterior to orbital margin, articulated, lateral carinae feebly developed, ventral carina obsolete, margin straight, with two small acute teeth on distal 3rd, with short plumose median setae proximally. Carapace smooth, glabrous, supraorbital spines absent, orbit feebly developed, inferior orbital angle strongly produced, distally blunt in lateral view, antennal spine well-developed, marginal, slightly exceeding inferior orbital angle, hepatic spine subequal to antennal spine, distinctly inferior to level of antennal spine, anterior to level of 1st dorsal rostral tooth, anterolateral angle of branchiostegite broadly rounded, not produced.

Abdomen as in *P. toloensis*, smooth, glabrous, 3rd tergite not posterodorsally produced, pleura broadly rounded, 6th segment c. $1.65 \times$ length of 5th, $1.9 \times$ longer than anterior depth, $0.75 \times$ of carapace length, posteroventral angle bluntly produced, posterolateral angle acutely produced. Telson (Fig. 1N) c. $1.1 \times$ 6th segment length, $4.0 \times$ longer than anterior width, lateral margins straight, posteriorly convergent, with two pairs of well-developed dorsal spines, at c. 0.45, 0.65 of length, posterior margin c. 0.5 of anterior width,

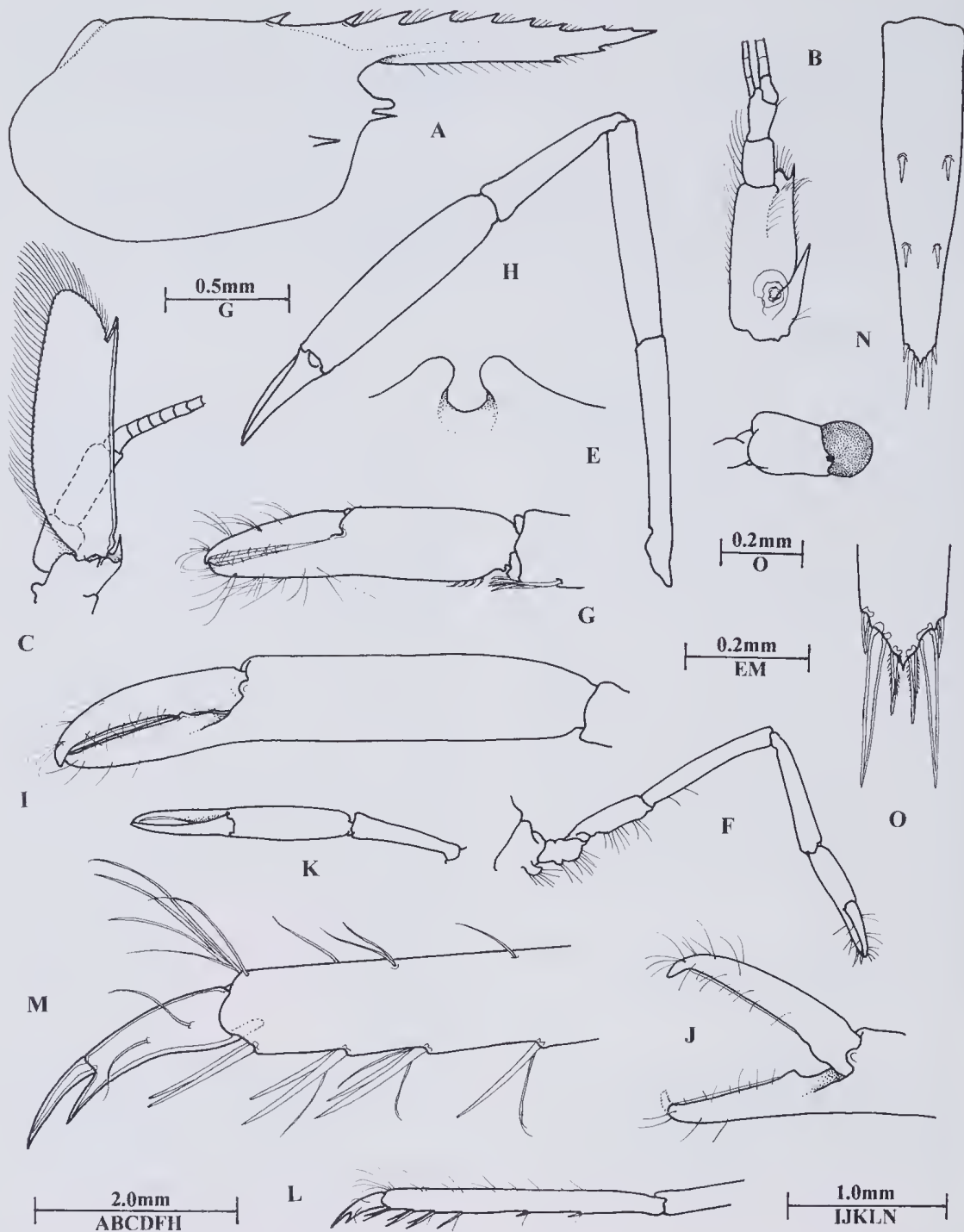


FIG. 1. *Periclimenes terangeri* sp. nov., ovigerous ♀ paratype (QMW22275), Polka Point, North Stradbroke I. A, carapace and rostrum, lateral. B, antennule. C, antenna. D, eye, dorsal. E, 4th thoracic sternite. F, 1st pereiopod. G, same, chela. H, major 2nd pereiopod. I, same, chela. J, same, fingers. K, minor 2nd pereiopod, carpus and chela. L, 3rd pereiopod, propod and dactyl. M, same, distal propod and dactyl. N, telson. O, same, posterior spines.

angular, with acute median point, lateral spines (Fig. 1O) subequal to dorsal spines, intermediate spines slender, c. 0.18 of telson length, submedian spines robust, setulose, c. 0.45 of intermediate spine length.

Antennular peduncle (Fig. 1B) normal, as in *P. toloensis*, proximal segment c. $2.2 \times$ longer than central width, with small acute ventromedial tooth, distolateral angle bluntly produced, with strong acute lateral tooth, extending well beyond distal margin of lobe, statocyst with irregular subcircular statolith, stylocerite slender, acute, reaching to c. 0.5 of segment length, intermediate and distal segments normal, combined lengths c. 0.7 of proximal segment length, upper flagellum with proximal 5 segments of rami fused, shorter free ramus with 5 segments, with 10 groups of aesthetascs, longer ramus and lower flagellum slender, filiform.

Antenna (Fig. 1C) as in *P. toloensis*, with basicerite with well-developed lateral tooth, carapocerite not exceeding proximal segment of antennular peduncle, c. $2.8 \times$ longer than central width, reaching to c. 0.45 of scaphocerite length, flagellum well-developed; scaphocerite c. $3.3 \times$ longer than central width, lateral margin straight with strong distolateral tooth, lamella broad, scarcely tapering, distally bluntly angular, far exceeding distolateral tooth.

Eye (Fig. 1D) with large globular cornea, diameter c. 0.2 of carapace length, with dorsal accessory pigment spot, stalk c. $1.5 \times$ longer than wide, $1.5 \times$ longer than corneal diameter.

Mouthparts of normal *Periclimenes* form, without special features. Third maxilliped with vestigial arthrobranch. Fourth thoracic sternite (Fig. 1E) without median process, with low transverse lamina with subcircular median notch; 5th sternite similar, with u-shaped median notch.

First pereopods (Fig. 1F) slender, merus reaching to middle of carapocerite, chela (Fig. 1G) to end of scaphocerite, with palm subcylindrical, c. $2.4 \times$ longer than deep, fingers slender, compressed, c. 0.8 of palm length, with small acute articulated tips, strongly hooked, cutting edges well-developed over distal half, entire, laterally situated; carpus c. $1.1 \times$ chela length, subcylindrical, c. $5.0 \times$ longer than distal width; merus distinctly longer than carpus, c. $1.2 \times$ chela length, uniform, $9.0 \times$ longer than central width; ischium c. 0.6 of merus length; basis normal; coxa with well-developed setose ventral lobe.

Second pereopods (Fig. 1H,K) dissimilar, unequal; major chela (Fig. 1I) c. 1.4 of carapace length, with palm subcylindrical, slightly compressed, smooth, c. $4.0 \times$ longer than central width, fingers (Fig. 1J) robust, c. 0.55 of palm length, dactyl c. $4.5 \times$ longer than deep, cutting edge unarmed, distal 2/3 of cutting edge lateral, entire, sharp, fixed finger similar, with single acute tooth proximally, cutting edge distally sharp, entire, tip missing; carpus c. 0.65 of palm length, $3.5 \times$ longer than distal width, tapering proximally, unarmed; merus longer than carpus, equal to 0.95 of palm length, 0.65 of chela length, unarmed, $7.0 \times$ longer than central width, subuniform: ischium c. $1.1 \times$ merus length, $10 \times$ longer than central width; basis and coxa without special features. Minor chela (Fig. 1K) c. 0.8 of carapace length, 0.65 of the major chela length; palm c. $3.5 \times$ longer than central width, subcylindrical, fingers c. 0.9 of palm length, more slender, proximal cuttings edge entire, tips acute, feebly hooked, carpus c. 0.95 of palm length, more slender; proximal segments similar to major chela.

Ambulatory pereopods slender; 3rd pereopod with dactyl (Fig. 1M) slender, c. 0.23 of propod length, simple, corpus c. $3.0 \times$ longer than proximal depth, compressed, tapering distally, dorsal margin convex, ventral margin sinuous, sharp, unguis distinctly demarcated, strong, curved, c. 0.65 of corpus length, deflexed; propod (Fig. 1L) c. 0.65 of carapace length, $12 \times$ longer than central depth, uniform, sparsely setose, distal 4th of ventral border with three pairs of long spines distally, c. $1.25 \times$ propod width, single similar spine proximally, proximal three quarters of ventral border with two short spines, carpus 0.5 of propod length, unarmed; merus 0.95 of propod length, unarmed; ischium 0.6 of propod length, unarmed, basis and coxa normal. Fourth and 5th pereopods similar to 3rd.

Uropod as in *P. toloensis*; protopod with small blunt distolateral lobe; exopod c. $3.0 \times$ longer than wide, lateral margin with slender acute distolateral tooth, with large mobile spine medially, dieresis feebly developed; endopod c. 0.9 of exopod length, c. $4.0 \times$ longer than wide.

MEASUREMENTS (mm). Holotype, QMW21735 ♀: carapace length, 2.4; carapace and rostrum, 4.9; total body length (approx.), 12.7; 2nd pereopod, major chela, 3.5; minor chela, 2.1; length of ovum, 0.5.

COLOURATION. No data.

HOST. Not recorded.

SYSTEMATIC POSITION. One of the *Periclimenes obscurus* species group, most closely related to *P. toloensis* Bruce, from which it may be distinguished by the following features:

1) more slender, acuminate rostrum, with two ventral teeth.

2) more elongate eyestalk, c. $1.5 \times$ longer than wide, compared with c. $1.0 \times$.

3) 4th thoracic sternite with transverse ridge with subcircular median notch.

4) 1st pereopod chela slightly shorter than carpus, distinctly shorter than merus, not longer than carpus.

5) propod of 3rd pereopod armed distally with 3 pairs of long slender spines, length exceeding distal propod width, and a single long ventral spine, more proximal spines short, not with shorter spines, with two distal pairs only.

6) dorsal telson spines subequal to lateral pair of posterior telson spines, not minute, much smaller than lateral posterior spines.

REMARKS. The holotype of *P. toloensis* was a ♂ from 10-30m off Ap Chau, Hong Kong, and was possibly associated with a gorgonian host (Bruce, 1969; 1982). The host has subsequently been identified as *Hicksonella princeps* Nutting, 1910 (Moreton & Harper, 1995). As the present specimens are both adult ♀♀, sexual dimorphism may account for some of the morphological differences. The holotype of *P. toloensis* had a POCL of 2.4 mm; it was therefore of similar size to *P. terangeri* (POCL 2.7mm) and probably also fully adult.

Periclimenes toloensis of Chace & Bruce (1993), from the Sulu Archipelago, from 38m, also an ovigerous ♀, is particularly similar to *P. terangeri* in that the dorsal telson spines are not minute but it has only a single ventral rostral tooth and the spinulation of the ambulatory propod resembles closely that of *P. toloensis*.

The specimens referred to *P. indicus* (Kemp, 1915), from intertidal anemones, *Macrodictyla aspera*, by Bruce (1983b) may also belong to the present species but are not available for re-examination. The species reported from Moreton Bay by Wadley (1978) as *Periclimenes (P.) nr obscurus* Kemp, 1922, may also belong to *P. terangeri*. Specimens provided by Dr Wadley have been examined but unfortunately no conclusions could be reached due to lack of many appendages.

Onycocaris stradbrokei sp.nov. (Figs 2-3)

ETYMOLOGY. From locality of capture, North Stradbroke I.

MATERIAL. HOLOTYPE: QMW21691, 1 ♀, stn QMP-6, Myora Reef, North Stradbroke I., Qld, 27°29'S. 153°25'E., 9m, on patch reef, coll. P. Davie and J. Short, 5 March 1996. ALLOTYPE: QMW22276 1 ♂, same collection data as holotype.

DESCRIPTION. Small shrimps of stout sub-cylindrical body form, generally similar to other *Onycocaris* species.

Female with rostrum (Fig. 2AB, 3A) short and broad, about as wide as long, reaching to level of anterior margins of eyes, unarmed, distally acute, slightly upturned, without distinct dorsal carina, lateral carinae expanded, ventral carina well-developed; orbital notch well marked, inferior orbital angle extracorneal, broadly acute; anterolateral branchiostegite broadly rounded.

Abdomen with pleura rounded, 6th segment with posterolateral angle acute, posteroventral angle larger, acute. Telson (Fig. 2J) $1.9 \times$ longer than broad, lateral margins convex, convergent, dorsal spines small, subequal, marginal, at 0.55 and 0.8 of telson length, posterior margin broadly convex, without median point, c. 0.25 of anterior width, posterior spines (Fig. 3F) short, small, lateral spines similar to dorsal spines, c. 0.45 of intermediate spine length, intermediate spines c. 0.1 of telson length, $5 \times$ than proximal width, with 3 submedian spines, feebly setulose, c. 0.6 of intermediate spine length.

Antennular peduncle (Fig. 2C) short, exceeding carpocerite and scaphocerite; proximal segment c. $2 \times$ as long as central width, with acute tooth distolaterally, without ventromedial tooth, stylocerite well-developed, acute, reaching to half segment length; intermediate and distal segments short and broad, combined length c. 0.55 of proximal segment length; upper flagellum short, feebly biramous, four proximal segments fused, distal part of 4th segment free, with 7 groups of aesthetascs, dorsal ramus with 7 slender free segments; lower flagellum short, with 12 slender segments

Antenna (Fig. 2D) with basicerite stout, laterally unarmed, with large protuberant process for antennal gland aperture; carpocerite well exceeding scaphocerite, c. $4.0 \times$ longer than central width, flagellum short, filiform; scaphocerite small, c. $2 \times$ as long as distal width, anterior margin broadly rounded, lateral margin straight

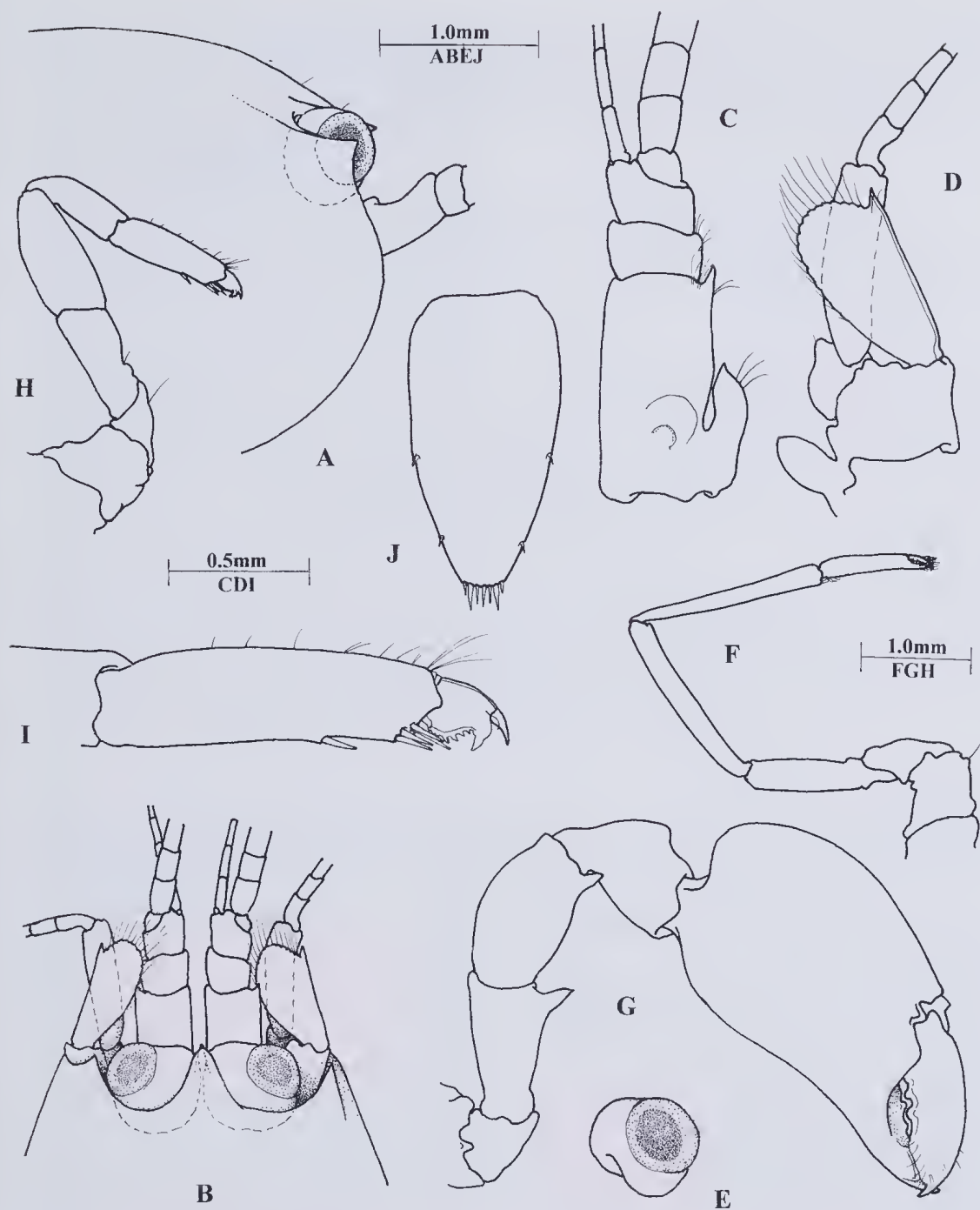


FIG. 2. *Onycocaris stradbrokei* sp. nov., ♀ holotype (QMW21691), Myora Reef, North Stradbroke I. A, anterior carapace, eye, and left antennular peduncle, lateral. B, anterior carapace, eyes and antennal peduncles, dorsal. C, antennular peduncle. D, antennal peduncle. E, eye, dorsal. F, 1st pereopod. G, major 2nd pereopod, lateral. H, 3rd pereopod. I, same, propod and dactylus. J, telson.

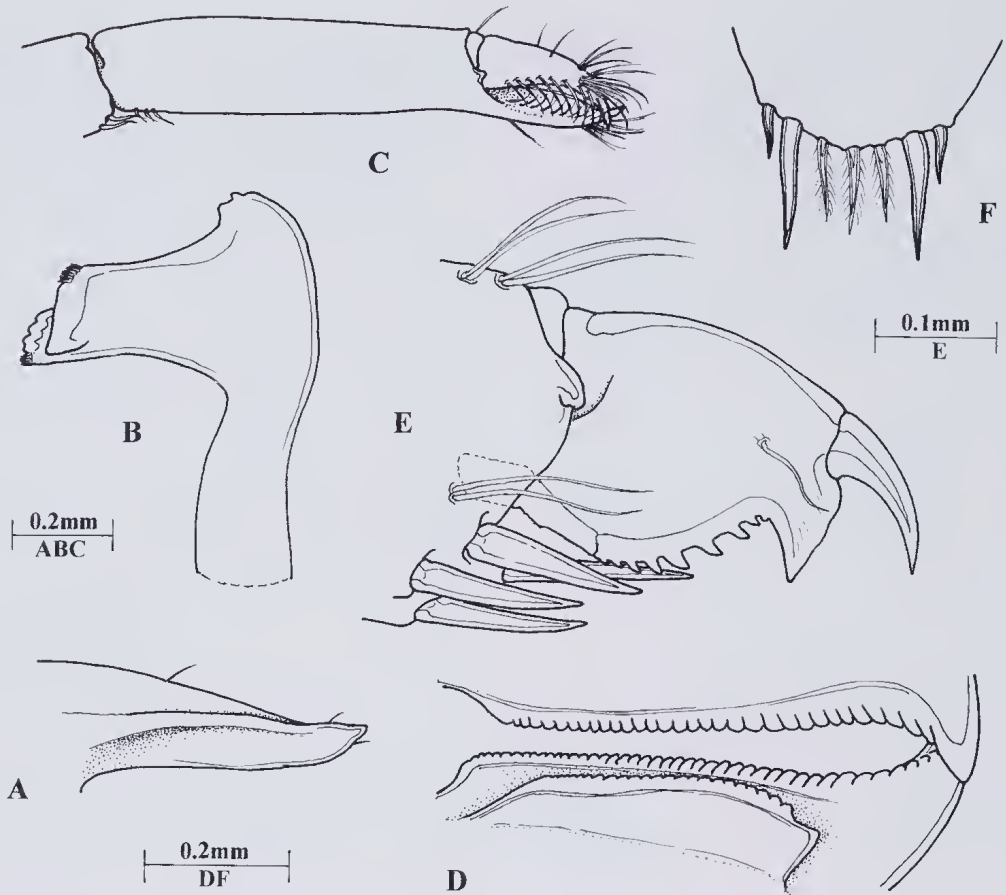


FIG. 3. *Onyccaris stradbrokei* sp. nov., ♀ holotype (QMW21691), Myora Reef, North Stradbroke I. A, rostrum, lateral. B, mandible. C, 1st pereiopod, chela. D, major 2nd pereiopod, distal cutting edges of fingers. E, 3rd pereiopod, distal propod and dactyl. F, telson, posterior spines.

with short stout distal tooth, not exceeding anterior margin of lamella.

Eyes (Fig. 2E) contiguous in midline, anterior margins subquadrate, with oblique hemispherical cornea, feebly pigmented, stalk short, globular, width c. 1.25 of corneal diameter.

Mandible (Fig. 3B) with slender corpus; molar process robust, distally obliquely truncate, feebly dentate, sparsely setose, incisor process strongly reduced, non-dentate. Posterior mouthparts present no special features. Thoracic sternites unarmed; very narrow, longitudinally carinate between 3rd pereiopods.

First pereiopod (Fig. 2F) long and slender, reaching beyond carapocrite by half merus, chela and carpus c. 0.65 of carapace length; chela (Fig. 3C) mooth, c. 4.0 × longer than central width, subcylindrical, slightly swollen centrally, fingers c. 0.35 of palm length, slender, very acutely

pointed distally, feebly subspatulate with entire medial cutting edges, with row of stiff setae along lateral edges; carpus slender, c. 1.75 × chela length, 9.0 × longer than distal width, tapering proximally; merus 1.8 × longer than chela, 8.0 × longer than central width; ischium 1.33 × chela length, 4.5 × longer than central width; basis c. 0.8 of chela length; basis stout, with small distoventral process.

Second pereiopods (Fig. 2G) well-developed, robust with large, stout, near subequal, vertically held chelae. Major 2nd pereiopod with chela c. 0.7 of carapace length, palm stout, smooth, compressed, broadly rounded posterodorsally, ventral border sinuous, c. 1.2 × longer than greatest depth, situated at c. 0.5 of length, tapering distally, dactylus c. 0.66 of palm length, 3.3 × longer than proximal depth, sparsely setose, with

strong acute tooth distally, medially concave with lateral cutting edge, proximal half with 2 small, low blunt teeth, distal half (Fig. 3D) convex with c. 30 small rounded teeth, size increasing slightly distally, fixed finger similar, with 3 small teeth proximally, c. 40 teeth (Fig. 3D) along distal cutting edge, slightly smaller than dactylar series, with well-developed submarginal flange distolaterally, with c. 23 small rounded marginal teeth and blunt distal angle, dactylar cutting edge closing into sulcus between flange and main cutting edge of fixed finger; carpus stout, c. $1.7 \times$ longer than greatest width, smooth, unarmed, distally broadened; merus stout, centrally swollen, without ventral tubercles, c. 0.6 of palm length, $1.8 \times$ longer than central width, with strong subacute distoventral tooth laterally; ischium slightly shorter than merus, tapering proximally, $2.0 \times$ longer than distal width, ventrally smooth, with very strong acute distoventral tooth laterally; basis and coxa robust, without special features. Minor 2nd pereopod similar to major; slightly smaller, chela c. 0.83 of carapace length, teeth along distal cutting edges of fingers slightly fewer and smaller.

Third pereopod (Fig. 2I) short, robust, extending beyond carpocerite by dactylus only; dactylus (Fig. 3E) strongly compressed, unguis distinct, acute, curved, c. 0.6 of dorsal corpus length, $2.5 \times$ longer than basal width, without ventral denticles, corpus c. $1.2 \times$ longer than greatest depth at 0.35 of length, dorsal and ventral borders strongly convex, ventral margin with large broad acute triangular distal tooth, with 8-9 small acute anteriorly inclined teeth proximally, central teeth larger than others; propod (Fig. 2I) c. 0.28 of carapace length, stout, $3.7 \times$ dactylar length, compressed, $3.7 \times$ longer than central depth, with 2 pairs of stout distoventral spines, single similar ventral spine at 0.6 of ventral length; carpus 0.75 of propod length, $2.8 \times$ longer than distal width, unarmed; merus $1.1 \times$ propod length, $2.6 \times$ longer than central width, unarmed, ischium subequal to propod length, $2.3 \times$ longer than distal width, unarmed; basis and coxa stout, without special features.

Uropods without special features.

Male generally similar to ♀, smaller and less robust, with relatively larger but similar chelae. Major chela c. $1.25 \times$ carapace length, minor chela subequal to carapace length; dentition of fingers similar, major chela with 4 small teeth proximally on fixed finger.

MEASUREMENTS (mm). Holotype, QMW21691 ♀, carapace length 4.25; total body length (approx.) 12, major chela, 3.85; minor chela 3.6. Male allotype, carapace length 2.8, total body length (approx.) 8.3, major chela 3.4, minor chela 2.8.

COLOURATION. Unknown.

HOST. Unidentified, presumably a sponge.

SYSTEMATIC POSITION. *Oncocaris stradbrokei* is most closely related to *O. bocki* Bruce, 1992, and may be distinguished by the following characters:

1) dactylar cutting edge of the major 2nd pereopod in *O. stradbrokei* has more numerous and distinctly smaller denticles than in *O. bocki*, of the same order of size as those on the fixed finger. In *O. bocki* there are less than 20 denticles, which are distinctly larger than those on the cutting edge of the fixed finger.

2) 3rd pereopod dactyl has more numerous ventral denticles (8-9), shorter, less erect, more inclined distally, the distal accessory tooth broader, more triangular, and with 2 pairs of stout distoventral propod spines, rather than 6 ventral denticles, a more slender based, trapezoidal accessory distal tooth, and a single pair of more slender distoventral spines with 3 ventral propod spines in *O. bocki*.

3) 1st pereopod is much more slender and elongate on *O. stradbrokei* than in *O. bocki*, with the carpus c. $1.75 \times$ the chela length as opposed to $1.4 \times$, propod $5.8 \times$ longer than central width, as opposed to $4.3 \times$ in *O. bocki*.

4) scaphocerite falling clearly short of distal end of antennular peduncle in *O. stradbrokei*, as opposed to subequal in *O. bocki*. Carpocerite markedly longer than scaphocerite in *O. stradbrokei*, shorter in *O. bocki*.

5) orbital notches deeper in *O. stradbrokei* than in *O. bocki*, so that tip of rostrum is level with anterior margins of eyestalks, with posterior part of eyestalk concealed. Eyes more fully exposed dorsally in *O. bocki*, (although this may possibly be due partly to post-mortem swelling).

REMARKS. *Oncocaris stradbrokei* is a member of the *O. aualitica* species group. This group has short toothless rostra and a strong distoventral tooth on the merus and ischium of the 2nd pereopods; it includes *O. aualitica* (Nobili, 1904), *O. amakusensis* Fujino & Miyake, 1969, *O. callyspongiae* Fujino & Miyake, 1969, and *O. oligodentata* Fujino & Miyake, 1969. *Oncocaris stradbrokei* and *O. bocki* may be distinguished

from other species by the non-denticulate ungues of the ambulatory dactyls. *Onycocaris aualitica* and *O. oligodentata* appear to be particularly closely related or are possibly synonymous. The species *O. amakusensis* and *O. oligodentata* have also been recorded from Australian waters.

***Periclimenaeus myora* sp. nov.**
(Figs 4-5)

ETYMOLOGY. From locality of capture, Myora Reef.

MATERIAL. HOLOTYPE: QMW21706, ovig. ♀, stn QMP-3, Myora Reef, North Stradbroke I., Qld, 27°29'S. 153°25'E., 3m, on patch reef, coll. P. Davie and J. Short, 5 March 1996.

DESCRIPTION. Small-sized pontonine shrimp of stout subcylindrical, slightly compressed body form.

Rostrum (Fig. 4ABC) slender, slightly depressed, short, c. 0.45 of carapace length, compressed without distinct lateral carinae, feebly up-curved, reaching to c. level of anterior corneal margins, falling well short of distal margin of proximal segment of antennular peduncle, dorsal margin with 3 acute teeth, 1st tooth well in advance of posterior orbital margin, shorter and stouter than two slender distal teeth, ventral margin convex, unarmed. Carapace smooth, depth subequal to length, without supraorbital spines or tubercles, antennal spine slender, acute, anterolateral angle of branchiostegite produced, rounded.

Abdomen without special features, stout, pleura 1-4 expanded, broadly rounded, pleuron 5 reduced, 6th segment broad, depressed, c. as long as anterior width, with posteroventral angles large, acute, posterolateral angles smaller. Telson (Fig. 4O) c. 2.0 × longer than 6th segment, 1.9 × longer than anterior width, lateral margins sublinear, posteriorly convergent, with two pairs of subequal, marginal dorsal spines, c. 0.07 of telson length, posterior margin c. 0.4 of anterior margin width, broadly convex, with three pairs of marginal spines (Fig. 5K), lateral spines robust, slightly smaller than dorsal spines, intermediate spines stout, 0.16 of telson length, 1.8 × lateral spine length, submedian spines slender, sparsely setulose, 1.2 × intermediate spine length.

Antennular peduncle (Fig. 4D) short, reaching to anterior margin of scaphocerite, proximal segment c. 2 × length of central width, with small distolateral tooth, without ventromedial tooth, stylocerite acute, 3.0 × longer than wide, reaching to c. 0.5 of segment length, statocyst normally developed, with granular statolith; intermediate and distal segments normal, combined length c.

0.6 of proximal segment length; upper flagellum with rami fused for three proximal segments, with 3rd segment partially free, with 8 groups of aesthetascs, longer free ramus with 6 segments, lower flagellum slender, short, with 9 segments.

Antenna (Fig. 4E) with stout unarmed basicerite, coxal region with protuberant antennal gland opening, carpocerite short, slender, c. 5.0 × longer than distal width, subcylindrical, slightly flattened, not exceeding anterior margin of scaphocerite, flagellum short, filiform; scaphocerite (Fig. 5B) small, reaching to end of antennular peduncle, distally broadened, 2.4 × longer than wide, lateral margin slightly convex, with small acute tooth distally at c. 0.8 of central length, anterior margin broadly rounded.

Eye (Fig. 4F) with well pigmented oblique, hemispherical cornea, diameter c. 0.2 of carapace length, without accessory pigment spot, stalk short stout, c. 1.3 × longer than wide, strongly flattened medially.

Mouthparts of normal *Periclimenaeus* form, without special features. Mandible with corpus slender, incisor process (Fig. 5A) not expanded distally, with 4 main teeth, most medial tooth with smaller accessory denticle medially, molar process slender, obliquely truncate distally with marginal fringe of short setae.

Thoracic sternites narrow, unarmed.

First pereopods (Fig. 4G) normal, not particularly slender, merus reaching beyond carpocerite by chela, carpus and distal 3rd of merus, chela (Fig. 4H) with palm subcylindrical, slightly compressed, 2 × as long as deep, fingers subequal to palm length, broad, blunt, spatulate, with minutely bidentate tips, distal cutting edges sharply carinate medially and laterally, entire; carpus subequal to chela length, 4.5 × longer than distal width, tapering proximally; merus c. 1.2 × carpus length, 5.0 × longer than central width, subcylindrical, feebly bowed and tapering distally; c. 0.6 of merus length; basis normal; coxa without ventral process.

Second pereopods (Fig. 4I) well-developed, unequal, dissimilar. Major chela (Fig. 4J) large, stout, c. 1.7 × carapace length, oval in section, not strongly compressed, 2.0 × longer than deep, tapering distally, smooth, glabrous, fingers c. 0.25 of palm length, sparsely setose, dactylus with dorsal margin semicircular, with stout acute tip, cutting edge with large molar process proximally, distally minutely serrate (Fig. 5C), fixed finger with large fossa proximally, distal cutting

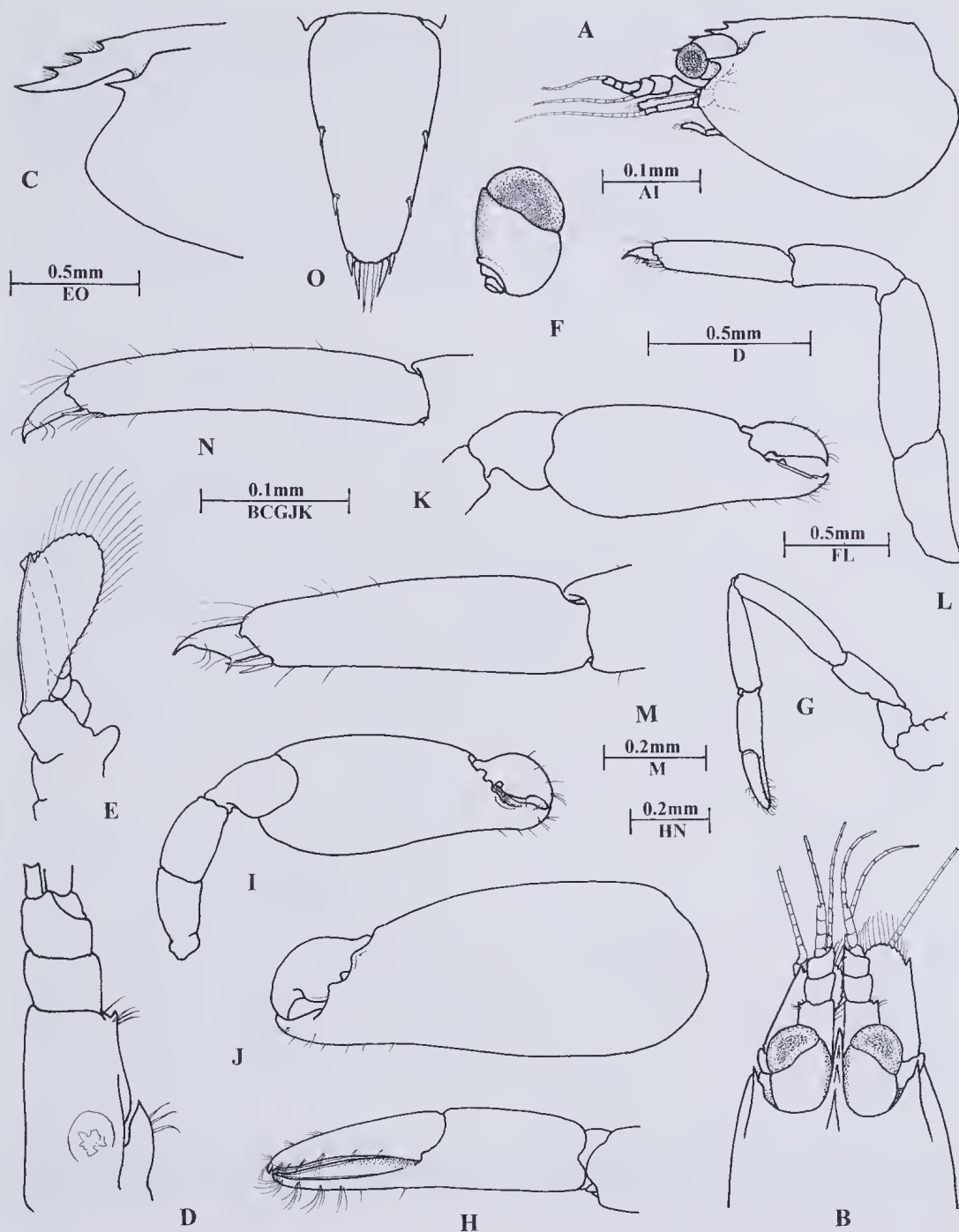


FIG. 4. *Periclimenaeus myora* sp. nov., ovigerous ♀ holotype (QMW21706), Myora Reef, North Stradbroke I. A, carapace and rostrum, eye and antennal peduncles, lateral. B, anterior carapace, eyes and antennal peduncles, dorsal. C, anterior carapace and rostrum, lateral. D, antennular peduncle. E, antennal peduncle. F, eye, dorsal. G, 1st pereopod. H, same, chela. I, major 2nd pereopod, medial. J, same, chela, lateral. K, minor 2nd pereopod, chela. L, 3rd pereopod. M, same, dactyl and propod. N, 5th pereopod, dactyl and propod. O, telson.

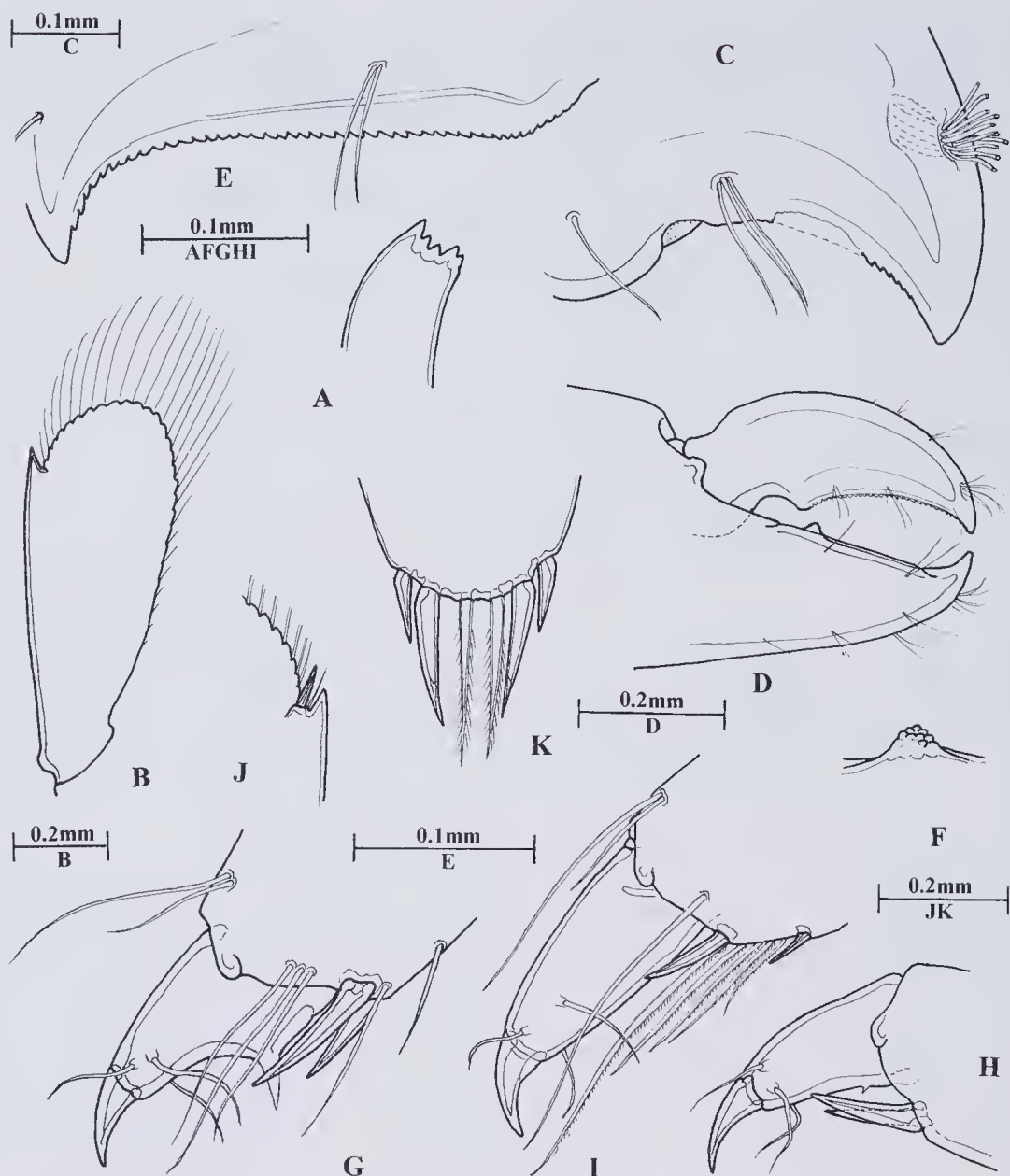


FIG. 5. *Periclimenaeus myora* sp. nov., ovigerous ♀ holotype (QMW21706), Myora Reef, North Stradbroke I. A, mandible, incisor process. B, scaphocerite. C, major 2nd pereiopod, distal dactylus. D, minor 2nd pereiopod, fingers. E, same, cutting edge of dactylus. F, same, fixed finger, cutting edge tooth. G, 3rd pereiopod, distal propod and dactylus. H, 4th pereiopod, same. I, 5th pereiopod, same. J, exopod of uropod, posterolateral angle. K, telson, posterior spines.

edge entire, tip stout, acute; carpus 0.33 of chela length, stout, distally expanded, unarmed; merus stout, 0.9 of carpus length, 1.6 × longer than central width, slightly expanded centrally, unarmed, ventral surface without tubercles or denti-

cles; ischium stout, subequal to carpus length, c. 2.0 × longer than distal width, tapering proximally, unarmed; basis and coxa stout, without special features. Minor chela (Fig. 4K) well-developed, stout, c. 0.66 of major chela length, 1.1

of carapace length, with palm strongly compressed, c. $1.8 \times$ longer than deep, smooth, sparsely setose, tapering slightly distally with fingers (Fig. 5D) curved medially, c. 0.4 of palm length, dactylus (Fig. 5E) $3.0 \times$ longer than deep, dorsal margin concave, cutting edge sublinear, with c. 40 minute, slightly recurved acute teeth, extending distally onto acute tip, fixed finger (Fig. 5F) with stout acute hooked tip, cutting edge straight, longitudinally cannulate, with entire edges, small tuberculate tooth proximally on medial edge; proximal segments as for major chela, smaller, less robust.

Ambulatory pereopods stout, 3rd (Fig. 4L) exceeding carpocerite by propod and dactylus (approx.), dactylus (Fig. 5G) 0.2 of propod length, distinctly longer than width of distal propod, unguis clearly demarcated, stout curved, c. $2.0 \times$ longer than basal width, unarmed, corpus c. $1.5 \times$ longer than basal width, compressed, tapering distally, with strong slender acute perpendicular tooth at 0.25 of ventral margin, distal ventral margin concave, 3 conspicuous sensory setae distally; propod (Fig. 4M) $3.6 \times$ longer than proximal width, tapering distally, sparsely setose, with pair of stout distoventral spines, lateral spine c. 0.15 of propod length, medial spine smaller, carpus c. 0.8 of propod length $2.7 \times$ longer than distal width, unarmed; merus c. $1.3 \times$ propod length, $3.0 \times$ longer than central width, unarmed; ischium 0.95 of propod length $2.5 \times$ longer than distal width, tapering proximally, unarmed; basis and coxa robust, without special features; 4th pereopod generally similar to 3rd, slightly more slender, dactylus (Fig. 5H) less deep proximally, ventral margin less concave with only minute proximal denticle, propod with pair of slightly unequal distoventral spines; 5th pereopod with dactylus (Fig. 5I) longer than in 3rd, c. 0.2 of propod length, corpus $2.0 \times$ longer than basal width, ventral margin feebly convex, unarmed; propod subequal to 3rd propod length, c. $5.5 \times$ longer than central width, with single distoventral spine and smaller preterminal spine.

Urpods without special features, protopodite distolaterally blunt, exopod (Fig. 5J) with lateral margin entire, unarmed, with small distal tooth and slender mobile spine medially.

MEASUREMENTS. (mm) ♀ holotype (QMW-21706), carapace length 1.8 total body length (approx.) 8.6; major chela, 3.1; minor chela 2.0, length of ovum, 0.55.

COLOURATION. Unknown.

HOST. Unidentified, presumably a tunicate.

SYSTEMATIC POSITION. *Periclimenaeus myora* is most closely related to *P. nobilii* Bruce, 1974, and may be distinguished by the following characters:

1) rostrum with 3 dorsal teeth in *P. myora* (only 2 in *P. nobilii*).

2) chela of the 1st pereopod is subequal to the carpus length (c. 0.8 of the carpus length in *P. nobilii*).

3) distal cutting edge of the major 2nd pereopod dactylus is minutely denticulate (entire in *P. nobilii*).

4) cutting edge of the minor 2nd pereopod dactylus is sublinear, with more uniform and numerous smaller teeth, about 40, (more sinuous with about 25 teeth, distinctly increasing in size distally in *P. nobilii*); chela ventrally glabrous (with numerous long setae in *P. nobilii*).

5) 3rd pereopod with dactylus 0.22 of propod lengthened much longer than distal propod depth (only $0.17 \times$ in *P. nobilii*) and subequal to distal propod width, ventral accessory tooth longer and more perpendicularly orientated; propod $3.6 \times$ longer than greatest depth (more swollen in *P. nobilii*, c. $3.0 \times$ longer than proximal width).

6) telson with dorsal spines marginal (subdorsal in *P. nobilii*), relatively smaller and shorter, c. 0.07 of the telson length (0.14 in *P. nobilii*), situated more posteriorly, anterior pair at c. 0.5 of telson length (0.3 in *P. nobilii*); lateral and intermediate posterior spines more robust, with more slender, longer submedian spines than in *P. nobilii*.

REMARKS. *Periclimenaeus nobilii* was described by Bruce (1974) on the basis of a single ♀ collected from an unrecorded locality in the Red Sea by Dr Félix-Pierre Jousseume in 1897, which had been examined by Nobili and identified as '? anomalie de *Coralliocaris hecate*' but not reported in published literature. There have been few subsequent reports. It is not certain whether the cutting edge of the fixed finger of the minor 2nd pereopod is longitudinally cannulate or not, but the illustration in Bruce (1974, fig. 14d) suggests that it may be. Two specimens from New Caledonia were referred to *P. nobilii* by Bruce (1991), but I am no longer convinced that these are conspecific and consider that two separate but closely related species are represented, both associated with related but different host tunicates. Differences, though small, are most marked in the ambulatory dactyls and propods. These two spe-

cies, together with *P. nobilii* and *P. myora* form a complex of closely related species probably all associated with related hosts of the tunicate family Didemnidae. *Periclimenaeus nobilii* has also been reported from La Réunion by Bruce (1983a) and the status of this specimen should be re-examined.

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- A NEW NAME, *THINORA*, PROPOSED FOR THE PREOCCUPIED NAME *THORINA* BRUCE (CRUSTACEA: DECAPODA: HIPPOLYTIDAE). *Memoirs of the Queensland Museum* 42(2): 398. 1998:- A new generic name was proposed for the hippolytid shrimp *Thor maldivensis* Borradaile, 1915 (Bruce, 1997). Professor L.B. Holthuis has kindly pointed out that the proposed name, *Thorina*, is preoccupied and therefore invalid. The name *Thorina* was first employed by Stephensen (1944) for a new deep-sea caprellid amphipod, *Thorina spinosa*.
- A new name, *Thinora*, an anagram, is now proposed to replace the invalid name *Thorina* Bruce, 1997. The type species of *Thorina* Bruce is *Thor maldivensis* Borradaile, 1915, by monotypy.

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A NEW SPECIES OF *FOERSTERELLA* DALLA TORRE (HYMENOPTERA:
TETRACAMPIDAE) FROM AUSTRALIA

CHRISTOPHER J. BURWELL

Burwell, C.J. 1998 06 29: A new species of *Foersterella* Dalla Torre (Hymenoptera: Tetracampidae) from Australia. *Memoirs of the Queensland Museum* 42(2): 399-402. Brisbane. ISSN 0079-8835.

The first Australian representative of *Foersterella* Dalla Torre, *F. australis* sp. nov. (Tetracampidae) is described and distinguished from the similar *F. scaposa* Bouček from Papua New Guinea. The males of both species are the only known tetracampids with a five-segmented antennal funicle. Like other species of *Foersterella*, *F. australis* is a solitary egg-parasitoid of a tortoise beetle (Chrysomelidae: Hispinae), parasitising *Cassida compuncta* (Boheman). □ Hymenoptera, Tetracampidae, *Foersterella*, *Cassida*, Australia.

Christopher J. Burwell, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 21 July, 1997.

During the course of a study on the parasitoids of some tortoise beetles, Chrysomelidae: Hispinae (Cassidinae of some authors), from south-east Queensland (SEQ), an undescribed species of *Foersterella* Dalla Torre (Chalcidoidea: Tetracampidae) was reared from the eggs of *Cassida compuncta* (Boheman). *Cassida compuncta* lays its eggs singly on the underside of leaves of *Ipomoea cairica* (L.) (Convolvulaceae) and a large series of the *Foersterella* sp. was obtained by sweeping the foliage of *I. cairica* at Long Pocket, Brisbane.

Species of *Foersterella* are known from Europe, Africa, India, Papua New Guinea (PNG) and Australia and as far as known are all endoparasitoids of the eggs of tortoise beetles (Bouček, 1988). There are no described species of *Foersterella* known from Australia although Bouček (1988) recorded one female specimen of an undescribed species from Western Australia (WA) in ANIC. This paper gives the first description of an Australian species of *Foersterella*.

Morphological terminology follows Bouček (1988). Acronyms for collections are as follows: ANIC, Australian National Insect Collection, Canberra; BMNH, Natural History Museum, London; QM, Queensland Museum, Brisbane; UQIC, University of Queensland Insect Collection, Brisbane; USNM, United States National Museum, Washington.

Order Hymenoptera
Family Tetracampidae
Foersterella Dalla Torre

Foersterella contains *F. reptans* (Nees) and *F. erdoesi* Bouček from Europe and *F. scaposa* Bouček from PNG. Bouček (1988) noted unde-

scribed species in Africa, India and Australia. *Foersterella flavipes* Förster (listed as the type species by most authors) is a junior synonym of *F. reptans* (Bouček, 1992).

In Australia, *Foersterella* can be recognised using Bouček's (1988) key to the genera of Australasian Tetracampidae. *Foersterella* closely resembles *Tetracampe* Förster but can easily be separated by the greatly widened scapes of the males. In addition, the pilosity on the pronotum and mesonotum in *Foersterella* is sparse and includes pairs of outstanding setae on the pronotum, median lobe of the mesoscutum and axillae (Bouček, 1988). In contrast, the pronotum and mesonotum in *Tetracampe* are regularly and rather densely pilose, without outstanding pairs of setae (Bouček, 1988).

Both *F. reptans* and *F. erdoesi* are endoparasitoids of the eggs in *Cassida* Linnaeus (Bouček & Askew, 1968). The biology of *F. scaposa* is unknown (Bouček, 1988).

Further information on *Foersterella*, including a redescription, synonymies and biological and distributional information, is given by Bouček (1958), Bouček & Askew (1968) and Bouček (1988).

Foersterella australis sp. nov.
(Figs 1, 2)

MATERIAL. Holotype ♀ (QMT41404), Long Pocket, Brisbane, 27°31'S 153°00'E. 12.xi.1994, C.J. Burwell. PARATYPES: (175) Queensland: St Lucia, Brisbane, 27°30'S 153°01'E, 1 ♀, 13.ii.1993, C.J. Burwell, ex egg *Cassida compuncta* (Boheman) (Hispinae) on *Ipomoea cairica*; same data as holotype except 1 ♀ (9.vi.1991), 2 ♂ (29.x.1994), 21 ♂, 14 ♀ (30.x.1994), 17 ♂, 6 ♀ (12.xi.1994) (all UQIC); same data as holo-

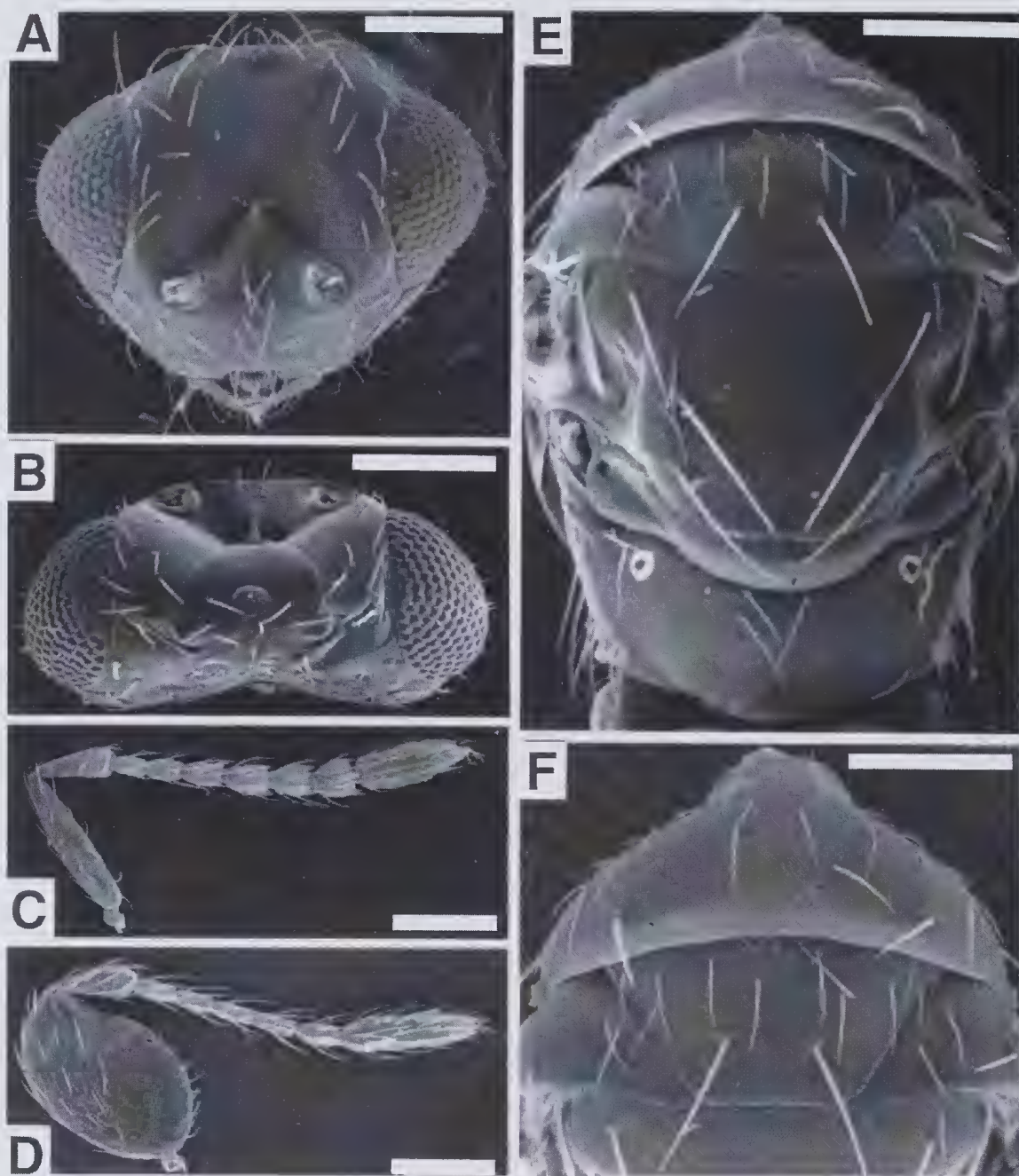


FIG. 1. *Foersterella australis* sp. nov. paratypes, Long Pocket, Brisbane, 12.xi.1994, C.J. Burwell (UQIC). A, ♀ head, anterior view. B, ♀ head, dorsal view. C, ♀ antenna. D, ♂ antenna. E, ♀ mesosoma, dorsal view. F, ♀ pronotum and mesonotum, dorsal view. Scalebars = 0.1mm.

type except ex egg *Cassida compuncta* (Boheman) on *Ipomoea cairica*, 1♀ (29.x.1994), 1♂, 1♀ (12.xi.1994) (all UQIC); same data as holotype except, 10.ii.1996, sweeping *Ipomoea cairica*, 5♂, 5♀ (ANIC), 5♂, 5♀ (BMNH), 5♂, 5♀ (USNM), 61♂, 19♀ (QMT41324-41403).

DIAGNOSIS. Male with antennal funicle composed of 5 segments. Median lobe of mesonotum with pair of outstanding, diverging setae and 5-19, but usually 16 or fewer, additional short setae. Lateral lobe of mesonotum with 3-5 short setae and a longer, posterolateral seta directed medially.

Female. Length 0.75-1.05mm, mean 0.91mm ($n=24$). Head, mesosoma and gaster black with green or brassy-green, metallic reflections. Scape and legs light yellow with apical tarsomeres brown. Pedicel and flagellum dark brown, first funicle segment often conspicuously lighter. Wings hyaline, veins light brown.

Head (Fig. 1A, B) 1.2-1.35 $\times$ as wide as high and 1.5-1.55 wider than frontovertex. Eye height about 0.6 $\times$ head

height. Malar space 0.5-0.6 $\times$ eye height. Lateral ocelli closer to eye than each other. Lower ocular line bisecting antennal toruli. Eye with sparse setae a little longer than diameter of facets. Face and frontovertex delicately engraved reticulate, scrobal grooves smooth.

Antenna (Fig. 1C) with scape about 4 $\times$ longer than wide and combined length of pedicel and flagellum 1.25-1.35 $\times$ head width. Pedicel equal to or a little longer than combined length of first and second funicle segments. Funicle 6-segmented, increasing in width apically. Antenna weakly clavate, club unsegmented, longer than pedicel, a little more than 2.5 $\times$ longer than wide.

Mesosoma (Figs 1E, F) 1.25-1.40 $\times$ longer than wide, dorsal surface, except on propodeum, delicately engraved reticulate with sparse setae on raised papillae. Pronotum bell-shaped, collar not delimited. Pronotum with sparse setae but bare posteromedially, posterolaterally with a pair of outstanding, weakly converging setae about as long as pedicel. Mesonotum 2.75-3.5 $\times$ wider than long. Median lobe with reticulation transversely elongated, usually 6-16 (19 in one specimen) short setae in anterior half to two thirds and medially to slightly posteromedially with a pair of outstanding, diverging setae about as long as those on pronotum. Lateral lobe with 3-5 but usually 4 short setae and a longer posterolateral seta directed medially. Axilla with a long seta on dorsal surface and 1-3 short setae. Scutellum 1.1-1.2 $\times$ wider than long, with reticulation longitudinally elongated, with 2 pairs of long, converging setae, the anterior pair about as long as antennal club and situated about medially. Scutellum slightly depressed just posterior of posterior pair of setae, forming transverse line. Propodeum smooth with 2-8 short setae anteromedially, callus with numerous setae.

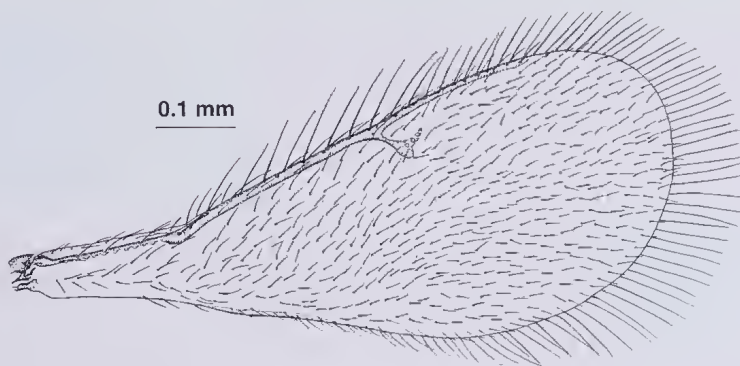


FIG. 2. *Foersterella australis* sp. nov. paratype ♀, Long Pocket Brisbane, 12.xi.1994, C.J. Burwell (UQIC). Forewing.

Fore wing (Fig. 2) 2.6-2.8 $\times$ longer than wide. Submarginal vein with 4 setae on dorsal surface. Marginal vein 1.05-1.20, 5.0-5.5 and 1.15-1.35 $\times$ as long as costal cell, stigmal vein and postmarginal vein respectively.

Gaster ovate, slightly longer than mesosoma, 1.5-1.8 $\times$ longer than wide in critical point dried specimens.

Male. Length 0.74-1.02mm, mean 0.86mm ($n=39$). Similar to female except scape light brownish-yellow, brown dorsally. Pedicel, club and usually third funicle segment dark brown. Fourth and fifth funicle segments light brown, second segment light brownish-yellow, first segment light yellow. Head 1.25-1.35 $\times$ as wide as high, 1.55-1.65 $\times$ as wide as frontovertex. Antenna (Fig. 1D) with scape greatly widened, 1.55-1.67 $\times$ longer than wide. Combined length of pedicel and flagellum 1.3-1.4 $\times$ head width. Funicle 5-segmented, segments about subequal, except fifth a little wider. Antenna distinctly clavate, club about 3.5 $\times$ longer than wide. Mesosoma 1.20-1.45 $\times$ longer than wide. Mesonotum 3.05-3.55 $\times$ wider than long, with 5-16 short setae. Scutellum 1.05-1.15 $\times$ wider than long. Gaster about as long as mesosoma, 1.45-1.75 $\times$ longer than wide in critical point dried specimens.

BIOLOGY. *Foersterella australis* is a solitary endoparasitoid in the eggs of the tortoise beetle *Cassida compuncta* which feeds on several species of *Ipomoea* L. and *Polymeria calycina* R. Br. (Convolvulaceae) in SEQ. The beetle lays its eggs singly, within membranous cases, on the underside of leaves. Only eggs laid on *I. cairica* have been found parasitised by *F. australis*. A second species of tortoise beetle, *Cassida diomma*

Boisduval, shares two larval-pupal parasitoids with *C. compuncta* and although *F. australis* has not been found parasitising *C. diomma* eggs to date, it is probably also a host.

DISCUSSION

There is a single female *Foersterella* from WA (4km SW Mining Camp, Mitchell Plateau, 14°52'S 125°50'E, 13.v.1983, I.D. Naumann, J.C. Cardale, ANIC) which closely resembles the specimens from SEQ. However until I see additional material, particularly males, I am reluctant to assign the WA specimen to *F. australis*.

Foersterella australis is closely related to *F. scaposa* Bouček from PNG. The antennae of males of both species are very similar and have only five funicular segments (Fig. 1D), a synapomorphy. Males of *F. erdoesi* and *F. reptans* have a 6-segmented funicle as do males of all other known tetracampids (Bouček 1988).

Foersterella australis differs from *F. scaposa* by its less setose mesonotum. Each lateral lobe of the mesonotum of *F. australis* has at most 5 short setae and the median lobe at most 19 but usually 16 or less short setae (Fig. 1F). The unique holotype male of *F. scaposa* (in ANIC) has 14 short setae on the left lateral lobe and 25 short setae (one lost) on the median lobe of the mesonotum. The more densely setose mesonotum of *F. scaposa* is unlikely to be due to allometry as the body length of the holotype falls within the range of males of *F. australis*. In addition the mesonotal

setae of *F. scaposa* are stronger and inserted on more prominent papillae than those of *F. australis*.

Variation in mesonotal setation of *F. scaposa* is impossible to assess until additional specimens become available. At such time a re-examination of the separate status of *F. scaposa* and *F. australis* may be necessary.

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A NEW TOOTH-PLATED DIPNOAN FROM THE UPPER DEVONIAN GOGO FORMATION AND ITS RELATIONSHIPS

K.S.W. CAMPBELL AND R.E. BARWICK

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The commonest dipnoan species from the Frasnian Gogo Formation are *Chirodipterus australis* Miles and *Griphognathus whitei* Miles. Less abundant species are *Holodipterus gogoensis* Miles and other holodipterids, *Pilliarhynchus longi* Barwick & Campbell, and *Gogodipterus paddyensis* (Miles). One would have expected many more representatives of tooth-plated forms of the *Dipterus*-type in the Late Devonian Gogo faunas. Recently a small number of individuals belonging to the tooth-plated group have been discovered, two of them being adults and one juvenile. They have been prepared to show how tooth-plates of this kind grew, and the outstanding features they produce in adults. They have been assigned to *Adoloplas moyasmithae* gen. et sp. nov. Histology of the tooth-plates has been investigated optically and by SEM. The cores of the teeth are composed of hypermineralised dentine with abundant dentine tubules; the pallial dentine is thick in the distal teeth where it is supported on a ring of pedestal dentine. The heels of the plates are composed of solid dentine of the kind that forms the core of the teeth. The basal pulp cavity is continuous beneath the tooth rows, but it is joined to the underlying bone at well defined patches. A Late Devonian (Frasnian) Canadian genus *Scaumenacia*, has been studied with a view to adding further information to a wider study of tooth-plate evolution. Consideration is given to the reasons why long-headedness has to be further analysed before it can be used for taxonomic purposes.

□ *Devonian, Dipnoi, tooth-plates, Gogo Formation.*

K.S.W. Campbell & R.E. Barwick. Department of Geology, Australian National University, Canberra, A.C.T. 0200, Australia; 5 January, 1998.

Acid-etched nodules from the Gogo Formation occasionally contain dental plates carrying real teeth. These teeth are not associated with intact skulls, as is usual for Gogo dipnoans; one well-preserved body indicated that a complete skull should have been present, had it been well-ossified. We have been reluctant to proceed with a description and taxonomic designation until more data on the skull roof became available. We have now etched most of the material available to us, and no well-ossified skull has appeared with teeth like those of the fragmentary material; consequently we are describing this material on the assumption that it will be some time before further specimens are discovered. The new information, though incomplete, is valuable for interpreting the Late Devonian history of the Dipnoi.

Three specimens are available — an adult and a juvenile held at the Geology Department, Australian National University (ANU) and an adult in the Western Australian Museum (WAM). The ANU adult was prepared from a nodule without first embedding it in plastic. As a result, all the parts are free and available for reassembly. The WAM specimen was split along the axis of the

fish at the time of collection. Because of this, it was embedded in plastic prior to etching, so that it could be better held together during preparation. Subsequently, the anterior part of one side of the preparation was treated with chloroform to loosen the plastic, and several isolated bones and a pair of tooth plates were obtained. These have proved especially valuable in understanding the histology of the tooth-plates. In the following discussion we have been able to provide separate descriptions of the macromorphology, micromorphology and histology of the tooth-plates of our new species.

SYSTEMATIC PALAEONTOLOGY

Order SPEONESIDRIONINA Campbell & Barwick, 1990

REMARKS. We continue to reject cladistic analyses that use all the so-called synapomorphic characters as of equal value in establishing relationships. We contend that a complete analysis of a group of taxa is much more likely to be achieved by an examination of a number of related functional characteristics. Our 1990 analysis indicated that during the Early Devonian, dipnoans used three different methods of covering the palate and

prearticular bones with dentine-bearing protuberances.

Denison (1974: 32) indicated that early dipnoan types had very different dental apparatuses, and that there was little indication "that 'plateless' genera were derived from nor closely related to those with dental plates". We considered that the three dental types referred to above, tooth-plated, dentine-plated and denticulate, are quite different in the organisation of other features in addition to the teeth, and once they were established they apparently did not alter from one type of organisation to another. This approach was attacked mainly because we did not regard the presence of denticles as always indicating a primitive condition, as though we had proposed the presence or absence of denticles in the mouth as the sole criterion of relationships. Although we used the dominance of denticles as a basis for naming one of the types, nowhere did we espouse the view that the presence of denticles is the sole defining feature of the group. To the contrary, we have pointed out that each type is organised so as to have a number of features correlated with the different types of food reduction (Campbell & Barwick, 1987, 1990; Barwick, Campbell & Mark-Kurik, 1997).

One of the three types outlined above had tooth-plates formed by teeth that were arranged in rows; new teeth having been formed at the distal end of each row. Members of this group we assigned to the Order Speonesydrionina. The teeth were described as having a cover of enamel (enameloid) over a thin layer of pallial dentine, which covered a thick and dense layer of heavily mineralised dentine. Dental plates of this type we have previously termed tooth-plated, as opposed to the dentine-plated types that had no true teeth at the plate margins (Smith & Campbell, 1987).

In a further criticism of our basic approach, Kemp (1992) has pointed out that some of the genera we assigned to non-denticulate groups, do in fact have teeth in the early growth stages, but have lost them in adulthood. She referred to the Late Devonian lungfish fossils from the Coffee Hill Member, Catombal, near Orange, NSW in which juveniles, up to 3mm x 4mm, some of which may have been *Chirodipterus*, may have had teeth in the early growth stages. In 1994 she considered that 'many lungfish of Devonian age, like *Chirodipterus*, previously regarded as having solid dental plates, are in fact built up from cusps that fuse at their bases to form tooth plates with radiating ridges. ... *Chirodipterus* is definitely one of the tooth plated lungfishes'. Nowhere has

she shown that *Chirodipterus* occurs in the Catombal fauna, a difficult thing to do in the absence of skeletal features other than tooth-plates. Until her material is described, and evidence of the existence of *Chirodipterus* of the *C. australis* type in the Catombal faunas is provided, we do not see that our analysis is in any way effected.

FAMILY INCERTAE SEDIS

REMARKS. In 1990 we separated late Palaeozoic tooth-plated dipnoans from *Dipterus* because they had no separate K bone, no lateral line in bone J, no buccohypophysial canal, unossified otic part of the braincase, and a partly buried pectoral girdle. *Adololopas* has a separate K, a canal in J, and an unossified braincase, but it lacks a buccohypophysial canal opening, and its girdle is largely buried. Hence it does not fall easily into the *Dipterus* group or the alternative non-*Dipterus* group on the characters defined in 1990. This view is supported by the elongate size of the cheek in the new genus *Adololopas*, the peculiar position of the lateral lines on the posterior part of the head, and the advanced nature of the dental plates with large basal pulp cavities. In addition it has a lateral line emerging from bone I to run along the body, a feature not observed in any other tooth-plated form apart from *Gnathorhiza*. We do not have access to the external parts of the mandible and the anterior part of the mandible which would also enable us to clarify the phylogenetic relationships. All this illustrates the difficulty of defining larger taxonomic groups on a number of characters which evolve considerably during time. Whatever the outcome, we now accept that *Adololopas* cannot be placed definitely in the Dipteridae, but we will not make a new Family to include it, because many features of the genus cannot be determined on present material.

Adololopas has a more advanced tooth-plate structure than *Dipterus*. Although *Dipterus* has for many years been regarded a member of the tooth-plated group, and forms assigned to it are very widely known throughout the world, the dental characteristics of specimens from the type locality are not very well preserved. Smith (1984) described the teeth of *Dipterus valenciennesi* from Scottish specimens. No other Middle Devonian genus showing the details of the tooth-plates has been described, but Elga Mark-Kurik has given us some incomplete Middle Devonian specimens. These are being described elsewhere in a separate paper (Campbell & Barwick, in press). These specimens provide an example of

the extent to which the plate structure had evolved during the Middle Devonian.

Adololopas gen. nov.

ETYMOLOGY. Greek *adolos*, true; Greek *lopos*, plate.

TYPE SPECIES. *A. moyasmithae* sp. nov. from the Frasnian (Upper Devonian) of the Gogo Formation, Canning Basin, Western Australia.

DIAGNOSIS. Endocranium poorly ossified. Dermal roofing bones not tightly sutured together, cosmine covered; bone B long and narrow, and with scalloped margins; bone I transmitting a lateral line canal from Y₁ to bone Z; no Y₂ preserved, but judging from the position of 8 and the shape of the opercular, it must have been present; bones 4, 5 and 8 unusually long for a tooth-plated form of this age; snout well-ossified. Adult pterygoidal tooth-plates thick, with an open median suture and with 6-7 rows of teeth; new conical teeth added at ends of rows, and mounted directly on bone; mandibular tooth plates showing teeth added sufficiently deeply to be out of occlusion but growing up into occlusion as they increase in size; adult tooth-plates with thin primitive dentine and serrated edges along the posterior margins; palatal tooth-plates concave, and mandibular plates convex. Juvenile tooth-plates with six or seven rows of sharp teeth; continuous rings of enamel- or enameloid-covered primitive dentine around the posterior, lateral and mesial edges. Parasphenoid with ploughshare shape, pointed posterior extremity and closed buccohypophysial canal lying in its anterior keel. Dentary narrow; angular bone with a deep notch posteriorly for articulation of the surangular. Body short and rapidly tapering; scales similar in form to those of *Chirodipterus australis*, but their size diminishes rapidly towards the tail and the dorsal margin.

REMARKS. This genus is noteworthy in having the lateral line canal running from bone I on the skull roof to the body. The only other genera in which this is known are *Gnathorhiza* and *Jarvikia* (Campbell & Barwick 1990, figs 4, 5). This interpretation of *Jarvikia* has been questioned by Schultze & Marshall (1993), who claimed that the connection of the main lateral line of the body with that of the skull roof through bone I is unique for *Gnathorhiza*. The specimen that shows the detail for *Jarvikia* is the paratype of *J. arctica* Lehman (1959, pl. 20B, fig. 22). One of us, KSWC, has examined Lehman's specimens, and considers that his photograph gives an incomplete impression of the lateral line canals. This inaccuracy is also shown in his figure 22. Herein we

produce new photographs of the same specimen showing the canals effectively (Fig. 2A,B). The canal runs posteromesially from the bone we interpret as Y into bone I (Campbell & Barwick, 1990, fig. 5). There the canal splits to produce a branch across bone B, and a second one backwards lateral to the process on the posterior end of the bone I, where it joins the main body lateral line canal. There is no other posteriorly directed canal from Y. The situation described is certainly unusual for the dipnoans, but we reject the statement of Schultze & Marshall (1993, p. 216) that our view on this feature is a 'mistake in our morphological analysis'. The new photographs show that the canal is clearly present as we have indicated. The palate of *Jarvikia* is not well known; Lehman (1959) recorded that the genus did not have tooth plates, but probably had a denticulated palate. One of us, KSWC, has been able to confirm that judgement by observation of the original specimens. The arrangement of the overlap between the pterygoids and the peculiar relationships of the parasphenoid, demonstrate that *Jarvikia* and *Adololopas* are distantly related. We see no reason to group these genera together on the basis of the posterior lateral line exit from the skull roof. On the other hand, the late Palaeozoic *Gnathorhiza* has totally different Y bones, and it has no lateral line canal in bone J; in addition it is unique in many other respects with which we dealt in 1990.

As has been indicated above, the second feature distinguishing *Adololopas* from other cosmine-bearing genera in the Gogo fauna is the presence of real teeth (Fig. 4). This takes it out of the group of *Chirodipterus* and *Pillalarhynchus* which also occur in the Gogo fauna.

The external dermal bones of the mandible of *Adololopas* are inadequately known, preventing detailed comparison with the bones of *Chirodipterus* and *Pillalarhynchus*. However, the angular (Fig. 8) has a deep and distinctive notch for the surangular, which must have had a different shape from the surangulars of *Chirodipterus* and *Pillalarhynchus*. We also infer that a splenial and post splenial were present in *Adololopas*, because of the shape and position of the anterior end of the angular. Thus it would be different from *Pillalarhynchus* in this respect also.

The arrangement of the scales is different from any other known Devonian dipnoan, in that they decrease dramatically in size a short distance behind the head and towards the dorsal margin. This indicates that, relative to its head size, the body was unusually short (Fig. 11). The wider

significance of this feature is unknown, because so many dipnoans are known from heads only. However, *Adololopas* is much shorter in the body than the other Gogo dipnoans, *Chirodipterus*, *Griphognathus* and *Holodipterus* in which we have adequate body preservation. *Pilliararhynchus* is more poorly known. *Dipterus* also is long bodied.

Finally, in connection with affinities, we note that *Adololopas* has a long cheek and a short snout. This type of structure was outlined by Schultze (1992), in his description of *Iowadipterus*, from the Givetian of Iowa, USA. It provided the basis on which he discriminated two types of long headed dipnoans, one type such as *Griphognathus* and *Rhinodipterus* which had long snouts, and the other such as *Iowadipterus* and *Holodipterus*, which had the post-orbital part of the skull elongated. Whereas we have no difficulty in distinguishing different types of long-headedness, we are unaware of its significance. *Adololopas* has long bones 4 and 5 and, judging from the shape of the snout and the palate, it would have been short-snouted. According to Schultze's criteria, it would be placed in the long-headed but short-snouted group. The problems raised by this assessment are dealt with below under the discussion at the end of the description.

Adololopas moyasmithae sp. nov.

ETYMOLOGY. In honour of Dr Moya Meredith Smith who has made a major contribution to the study of Palaeozoic dipnoan dentitions.

MATERIAL. HOLOTYPE: ANU49213, an incomplete specimen with part of the skull preserved. **PARATYPES:** WAM931.1.221, a specimen with part of the body and some skull, mandible and tooth plates preserved; and ANU49215, a small incomplete snout with the palatal and mandibular tooth-plates preserved; all from the Gogo Formation (Frasnian), Paddys Spring Valley. The two adults are so similar in structure of the tooth-plates and the cosmine on the external plates, that we see no reason to think that they are different species. The juvenile has tooth-plates in which the teeth are added at the ends of the tooth rows, successive growth of tissues at the tooth-plate margins similar to the adults, and with 6 or 7 tooth rows. All of these features are distinct from any other members of the other dipnoans in the fauna, that we can only consider all three specimens to be conspecific.

DIAGNOSIS. As for the genus.

DESCRIPTION. *Skull Roof.* Roofing bones are weakly joined at sutures, falling apart readily during etching (Figs 1, 4H,I, 5). Cosmine covers bones, except at the bone margins. Bone B is elongate, with a scalloped margin and with a pair

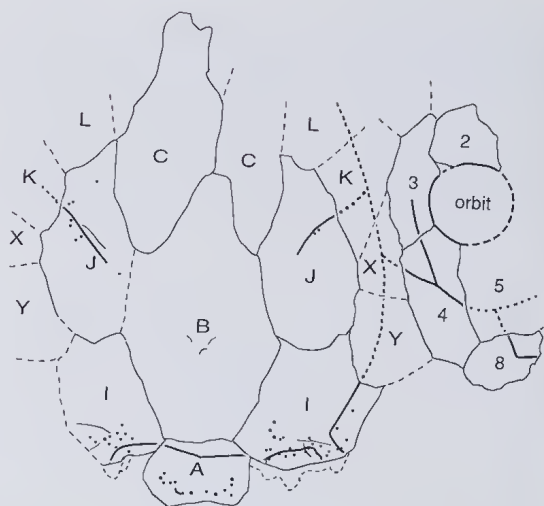


FIG. 1. *Adololopas moyasmithae* gen. et sp. nov. An outline sketch of the skull roof and part of the cheek drawn from the holotype, Fig. 4G-I. The cheek is situated in relation to the skull because the lateral line in 4 is displayed in X-rays and indicates the approximate position of the centre of ossification of X, and Y is placed to receive the lateral line from I. Scale = 10mm.

of centrally situated pit-lines; thickening for the attachment of the median crista is restricted to the anterior half of the plate. Bone I is transverse; posterior process on I for articulation of the ancleithrum is small; position of operculum and bone 8 indicate that Y₂ must have been present, and was loosely articulated (Fig. 3C); bone Z fitted into a groove in the posterior and posterolateral margin of I. Lateral line canal enters bone I anterolaterally, runs to its centre of ossification, and then turns abruptly posterolaterally to exit into a loosely articulated Z (Figs 1, 5). Two pit-lines present on bone I, an elongate transverse one and a short posterolaterally oriented one, the two not meeting. Cartilage attaching dorsolateral crista to roof present only to the anterior part of I and extends on to posterior part of J. Anterolateral edge of I has a deep angular embayment, defining the edge of the Y₁ bone into which the lateral line passes. Bone A is transverse, roughly hexagonal, and carrying the occipital commissure; numerous sub-branches of the canal extend backwards as shown on the X-radiographs (Fig. 5); this commissure continued through bone I as a short arc. Elongate bone J is preserved on both sides and carries a lateral line canal from its centre anterolaterally to an unpreserved bone; this must have been a bone K, which was a large bone whose outline is best defined on the left side; an elongate

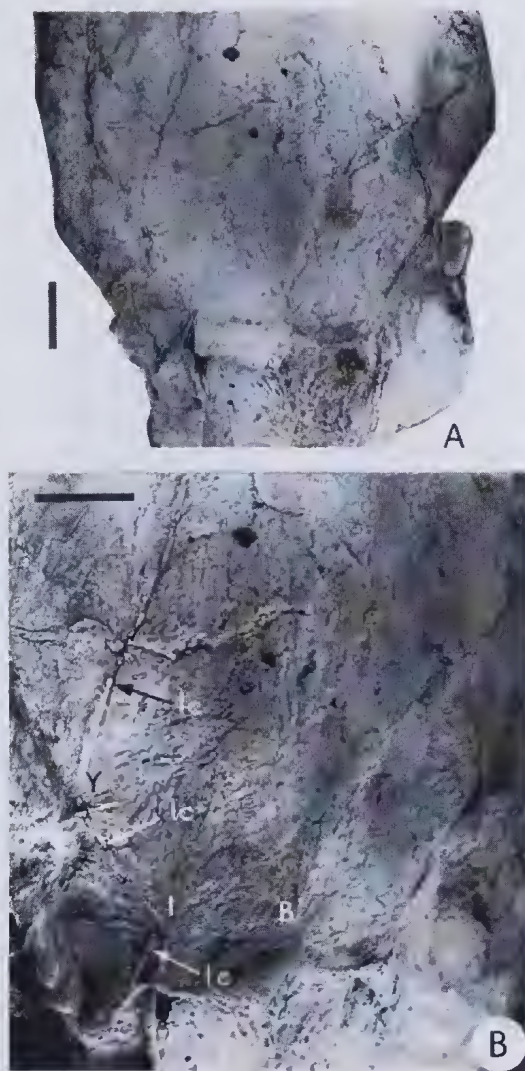


FIG. 2. *Jarvikia arctica* Lehman. This is the specimen figured by Lehman (1959, Pl. 20B). A, posterior part of the roof figured dorsally. B, enlargement of same, tilted to the right and laterally illuminated to show the lateral line canals, labelled lc. The centres of ossification of bones B, I and Y are labelled. The lines at the back of the specimen were produced by needle scratches. The bones are labelled and the canal runs off the back of the skull as shown. The extension at the back of bone I is incomplete. Scales = 10mm.

pit-line is also present on J. Bones C elongate and so shaped that any D present would have been small; other bones in front of Cs and on the cheek unknown, apart from some circumorbitals; lateral line canal present on bone 3; bone 2 short; bone 4 unusually long for a dipterid-like animal (Figs 1, 4G), extends from orbit almost to the opercular.

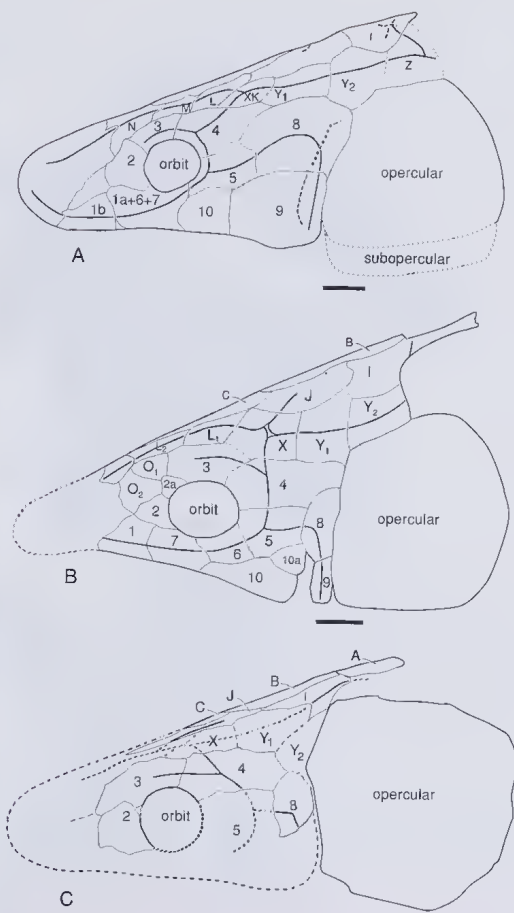


FIG. 3. Comparison between the lateral views of A, *lowadipterus*. B, *Holodipterus*. and C, *Adololopas*. *lowadipterus halli* is redrawn from Schultz (1992, fig. 10); *Holodipterus* is drawn from *H. (Asthenorhynchus) meemannae* (Pridmore et al., 1994). *Adololopas moyasmithae* is reconstructed from ANU49213. Note the difference in the positions of bones 4, 5 and 8.

Lateral line enters 4 from an anterodorsal rather than a posterodorsal direction, indicating that X is situated further forward relative to the orbit than in other dipterid-like animals; contact between X and J defined by projections on both sides of the specimen. Bone 8, which has been recognised by the angular bend in the lateral line and the finished edge against the opercular, is also longer than in other dipterids. Orbit 18% of length of skull from rear of B to front of C.

We have two isolated snouts, an adult from ANU49213 (Fig. 4J, K) and juvenile ANU49215 (Fig. 7A, B). Adult broad, and showing all the main features of other Devonian dipnoans of the

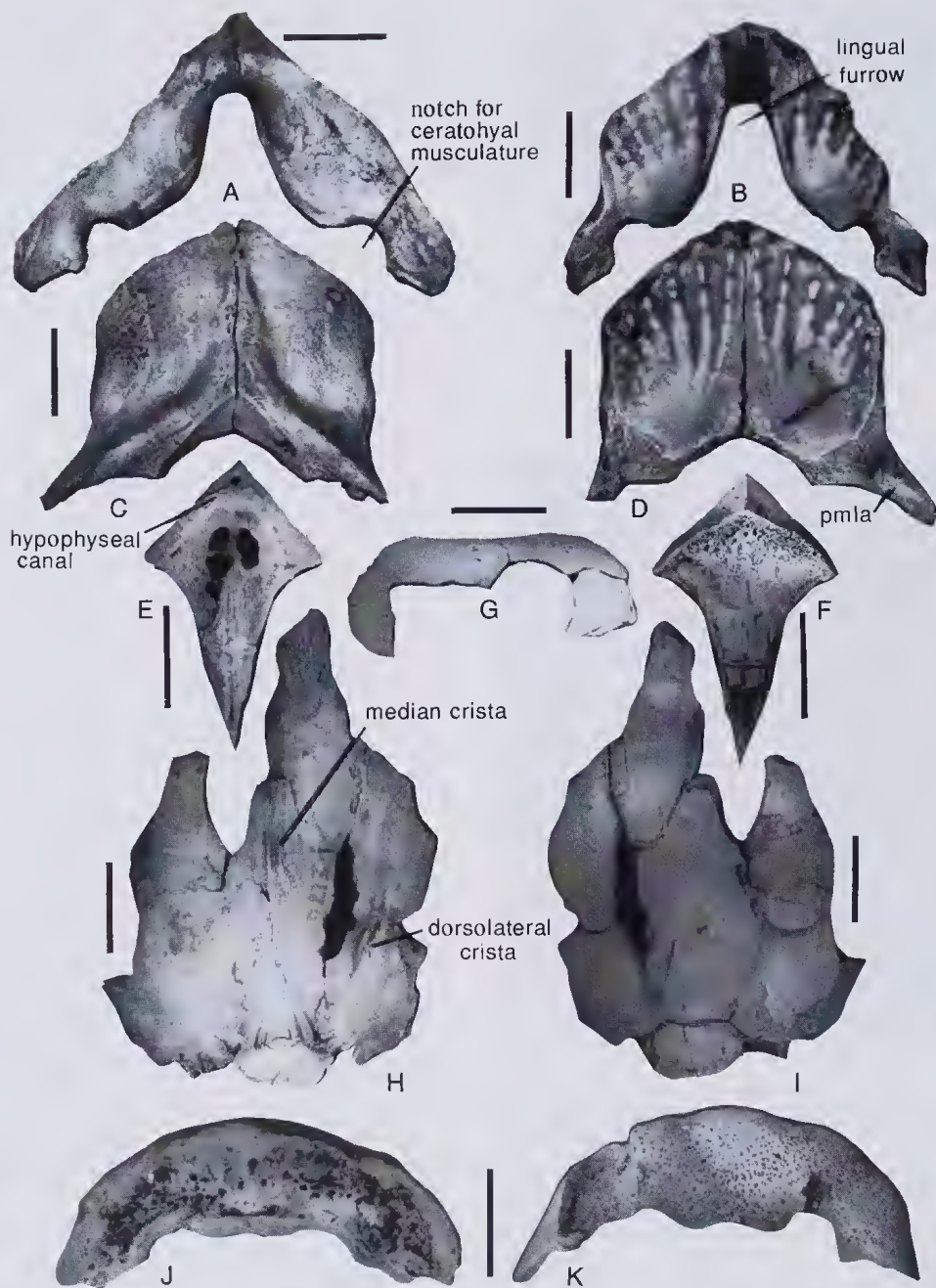


FIG. 4. *Adololopas moyasmithae* gen. et sp. nov. holotype. A, B, ventral and dorsal views of the prearticulars and tooth plates. C, D, dorsal and ventral views of the pterygoids and tooth plates. pmla = pterygoid-mandibular ligament attachment. E, F, dorsal and ventral views of parasphenoid isolated during preparation. Note the foramen in the anterior end for the buccohypophysial canal. G, lateral view of the orbit and the cheek plates. H, I, ventral and dorsal views of the posterior part of the skull roof. The left side of I is incomplete, but the bones on the right have complete edges. Note the attachment of the dorsolateral crista beneath the anterior end of bone I and the posterior end of bone J on the left side of H. J, K, posterior and anterior views of the isolated snout. Note the variation in the size of pores in the snout in K. Scales = 10mm.



FIG. 5. *Adololopas moyasmithae* gen. et sp. nov. X-radiograph of the posterior part of the skull of the holotype, photographed in ventral view. The entry points of the lateral lines into the bones are marked with arrows. Note also the branching of the lateral line canal in bone A (see Figs 1 & 4H). Scale = 10mm.

dental-plated types; external nares well separated, leaving only a small edge of tissue between them and the lateral labial pit; lateral line canals defined by the enlarged pores; juvenile snouts more highly arched than those of adults.

Palate. Pterygoid thinnest towards the anterior margin, thickening gradually posteriorly; dorsal palatal process present but depressed, with a bevelled dorsal surface inclined downwards laterally and a sharp crest along its mesial margin; bevelled surface without a periosteal layer, and exposing coarser textured bone than elsewhere (Fig. 4C); a rounded ridge adjacent to the mid-line increasing in height posteriorly and turning posterolaterally along the quadrate ridge; towards the mandibular articulation the quadrate ridge becomes narrower and sharper; lateral extremity turned down sharply towards the mandibular articulation; scar for pterygo-mandibular ligament well developed, and laterally placed on the quadrate.

Included with ANU49213 are five small isolated palatal plates, one being a median anterior



FIG. 6. *Adololopas moyasmithae* gen. et sp. nov., holotype. Isolated tooth plates from the anterior palate. A, median anterior plate showing the lines associated with new growth. B, C, pair of dermopalatine plates (in C the mesial anterior end is broken off); both show growth lines. D, E, another pair of plates of unknown origin from the same etch. Scales = 1.0mm.

and two others being symmetrical dermopalatines (Fig. 6); the remaining two are possibly other anterior tooth plates (Miles, 1977, fig. 72); median plate convex ventrally and carrying incremental layers of primitive dentine, forming marginal concentric outlines (Fig. 6A); these outlines do not continue around the entire margins without breaks; however, their distribution indicates that the median plate was not in contact with the adjacent pterygoid plates; central parts of all small plates include areas within which the dentine is darkened by apparently hypermineralised dentine. Parasphenoid of ANU49213 well preserved (Figs 4E,F); anterior face high and plough-share shaped; buccohypophysial canal situated in anterior corner, but does not open into the buccal cavity; posterior part of plate acutely triangular in outline, and with a long crest along its dorsal surface; central part of plate consisting of an open meshwork of bone.

Neurocranium unossified except at the anterior margin where tubules related to the anterior sensory systems are present.

Mandible. Mandible known from prearticulars and tooth plates of two adults and one juvenile, a small adult fragment and one adult angular. Lingual furrow of adult deep and barrel shaped (Figs 4A,B, 22A,B), slightly overhung by the tooth-

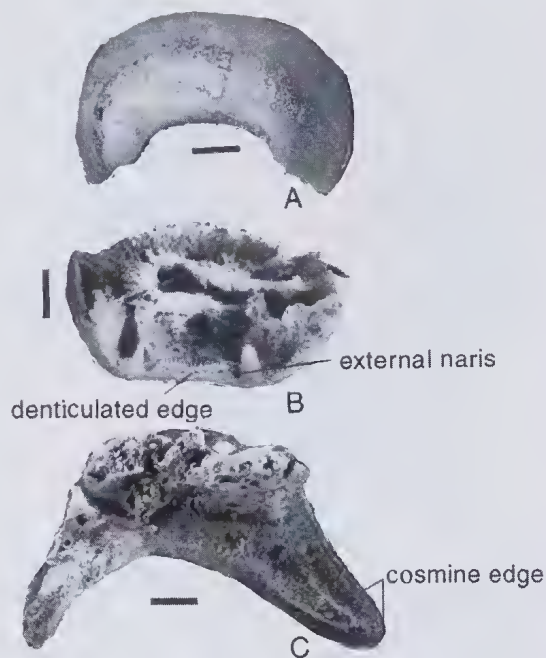


FIG. 7. *Adololopas moyasmithae* gen. et sp. nov. A, B, snout of ANU49215 in anterior and posterior views showing the high curvature. External naris labelled; pores for anterior commissure clear. C, internal view of broken dentary of the holotype. Note the edge of cosmine on the lateral and posterior edge, indicating the fact that it had no continuous bone junction with the surrounding bones. Scales = 2.0mm.

plates, and with a well rounded floor; junction between the two plates formed of bone without dentine; strong, rather sharp lateral projection of prearticular in front of the glenoid fossa (Figs 4B, 10B); pterygo-mandibular ligament attachment producing a small flange immediately medial to the glenoid fossa; between this flange and the back of the tooth plates is a deep gap for muscles

connecting to the ceratohyal (Fig. 4A,B). Small isolated incomplete dentary (Fig. 7C) shows the posterior end completely isolated from the infradentaries, and having some small blisters of bone indicating that addition to the edge of the bone was taking place.

Angular, represented by an isolated external bone of WAM931.1.221, with an edge indicating that it bordered the adductor pit, and carries two lateral line canals (Fig. 8A,B); shape of this infradentary is unusual, having a deep posterior notch in which the lateral line emerges at its apex; lower lateral line enters the bone about 5mm from the posterior edge and runs forward slightly, converging on the other canal; position of infradentary bone can be determined from the opening for the adductor fossa and the large upturned surface forming the contact with the process on the prearticular in front of the glenoid fossa; shape of the surangular notch and the position of the edge of the adductor fossa, indicate that the surangular was short; shape and position of angular suggests that both splenial and postsplenial were present to occupy the space between the mid-line and the angular.

Pectoral Girdles. Two pectoral girdles, one more complete (Fig. 9A,B) from ANU49213, and the cleithrum only on WAM931.1.221 (Fig. 9C); three other smaller fragments are known. Cleithrum with a deeply concave external surface, its anterior rim standing high, sharply defined and with (Figs 9C, 11A,B) or without (Fig. 9A,B) a large number of pustules; posterior half of external surface covered with moderately developed rough surface features; ventral extremity acute and with an angular excavation for the articulation of the clavicle; branchial lamina standing at a high angle to the external lamina, concave on its anterior face, and carrying a number of sharp projections into this concavity; dorsal

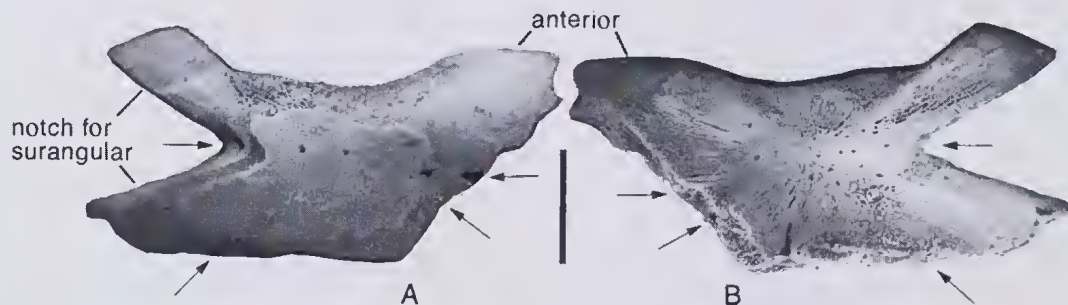


FIG. 8. *Adololopas moyasmithae* gen. et sp. nov. A, external and B, internal views of an isolated angular bone from WAM931.1.221. Position of mandibular and oral canals marked by arrows. Notch for surangular with a margin unaltered by etching. Opening for adductor muscles obvious at top of photograph. Scale = 10mm.

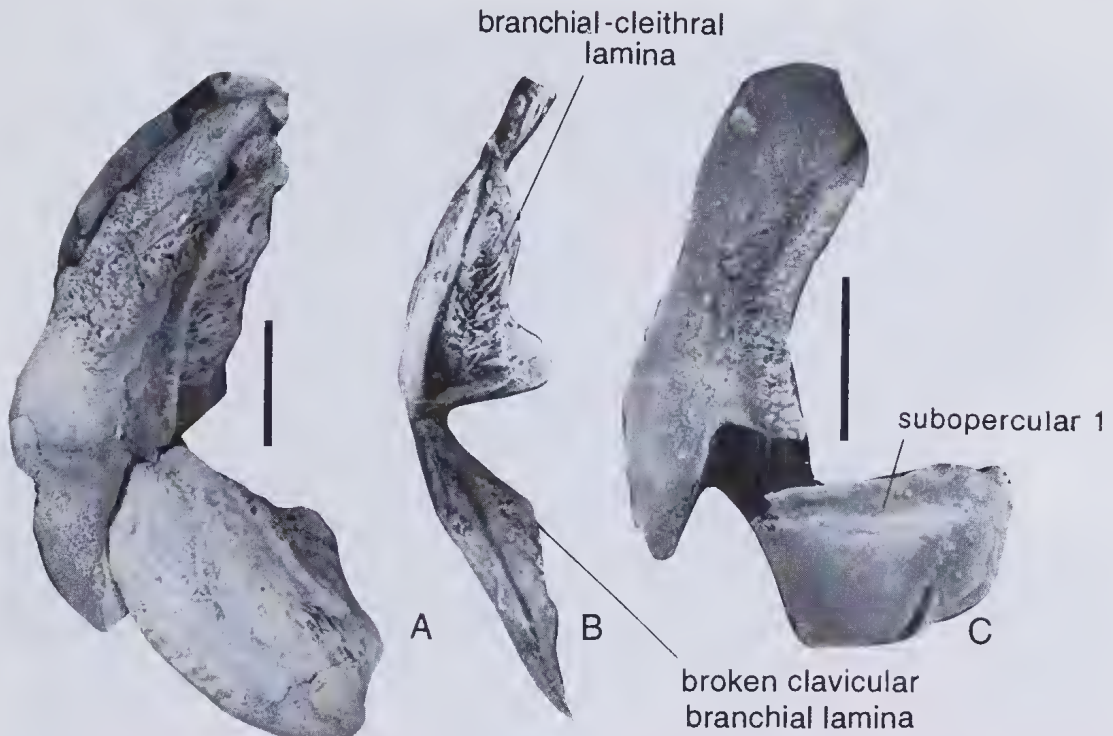


FIG. 9. *Adololopas moyasmithae* gen. et sp. nov. A, B, lateral and anterior views of an incomplete right pectoral girdle of the holotype. In A and B the branchial lamina on the clavicle is incomplete. C, cleithrum and the subopercular 1 of WAM931.1.221. Note the difference in ornamental pattern between this specimen and that of A. Scales = 10mm.

edge of lamina meeting the anterior edge of cleithrum about 8mm short of dorsal edge; ventral edge of branchial lamina thickened and bearing a distinct groove for the articulation of the clavicular branchial lamina. Clavicle with a much less concave external lamina and a weaker anterior rim than the cleithrum; ornament well developed on the anterior rather than the posterior half; ventral end of external lamina with a cutaway edge that continues up into the branchial lamina, producing an over-lapped surface presumably for the interclavicle; branchial lamina incomplete, but extending nearer to ventral edge than in *Chirodipterus australis*; originally it continued up to meet the cleithral branchial lamina along its entire length.

Operculars and Gulars. Opercular subquadrate in outline; leading edge almost straight ventrally (Fig. 10A,B), but turned posterodorsally on the upper edge; in anterior view, dorsal part of operculum bent medially; anterior edge of this in-turned part of bone abutts the posterior edge of the Y2 bone; the inward turning of the operculum demonstrates that the rotational edge lay ventral

to the upper edge of bone 8; this articulatory edge with slight overlapped margin, indicating the position of movement against the skull; posteroventral edge also slightly truncated; dorsal edge also overlapped; surface with strong Westoll lines.

Subopercular 1 with a strongly overlapped dorsal edge and a slightly ventrally curved ventral edge (Figs 9C, 10B); remainder of surface covered with cosmine apart from marginal resorption. Subopercular 2 not well-known, only partly exposed (Fig. 10B), but with overlap edges on both dorsal and ventral edges.

Principal gulars (Fig. 10B) generally ovate in outline, but with a strong point anterolaterally; about 18mm long and 18mm wide; anteromesial edge with a long undivided overlap which indicating a large median gular; lateral overlaps not completely clear, but indicating a submandibular and possibly a lateral gular; three Westoll lines on the surface; a transverse pitline 4mm long situated anteromesially on the plate.

Pectoral Fins. External ornament of the right pectoral fin partly preserved on WAM931.1.221 (Fig. 11A,B); individual scales small, cosmine

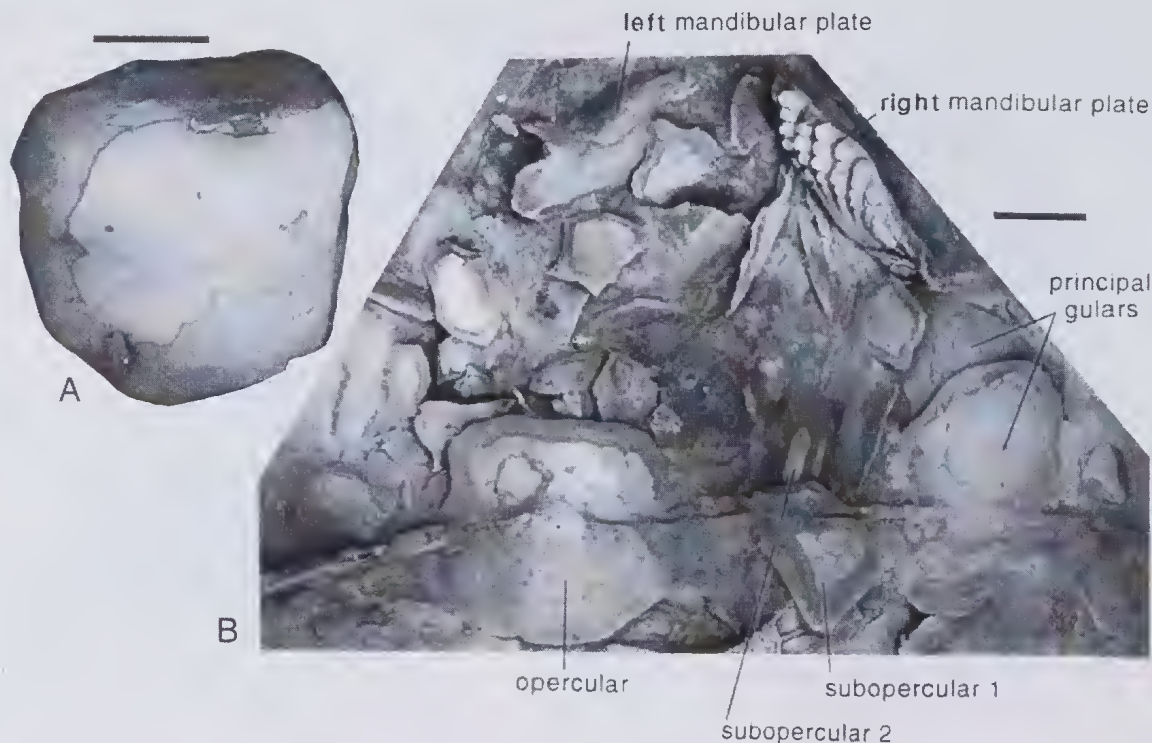


FIG. 10. *Adololopas moyasmithae* gen. et sp. nov. A, an isolated operculum of holotype; anterior to the right. B, WAM931.1.221, anterior part of specimen showing opercular, gular, subopercular 1 and 2 and mandibular plates. Scales = 10mm.

covered but with a small overlapped edge on some individuals; preserved part of fin 22mm long; occasional scales preserved on the inside of the limb (Fig. 11B); individual scales highly variable in outline; overlaps slight; probably only two or three rows of scales down the midline of the fin, but there may have been a smaller row on each side; no rays preserved.

Scales. Scales thin, cycloid in shape, and almost equidimensional in outline; inner surface with concentric growth lines; exposed surface with cosmine; size of scales decreases rapidly in both dorsal and posterior directions; on the flanks only 100mm behind the head, the length of the cosmine cover is only half of the forward scales (Fig. 11A); scale overlap is large (Figs 11A, 12). Scales immediately posterior to the cleithrum show no sign of cosmine (Fig. 11A,C). Like the cleithrum itself, they must have been buried beneath a thin layer of soft tissue.

DESCRIPTION OF TOOTH-PLATES. *Macromorphology of Juveniles.* At the early growth stages, the palatal plates show very narrow bands of shiny (probably enamel-covered) dentine along the posteromesial edge, and these abruptly

expand to form large flat surfaces anteromesially (Figs 13, 14). These bands are continuous around the posterior edge of the plate to the lateral margins where the inner ones progressively disappear, or can be faintly traced turning inwards between the teeth. The two outermost bands are quite clearly in two discontinuous units (Fig. 13C,D). The posteriormost one is replaced by another band which continues around the anterior margins of the plate, and carries the succession of teeth upon its surface. The band swings back between the teeth on the anterior edges (Figs 13A, 14C). There is no precise correspondence between the marginal bands and the addition of new teeth (Figs 13A,B). It is obvious that six teeth are added while four marginal bands were growing (Fig. 13B). The situation on the right plate is not so clear because of weathering, but the bands of tissue running across the plate surface are well marked (Fig. 13A). There is no sign of clear resorption and replacement of any bands, but more mineralised dentine of the plate has grown into some of the inner bands in places.

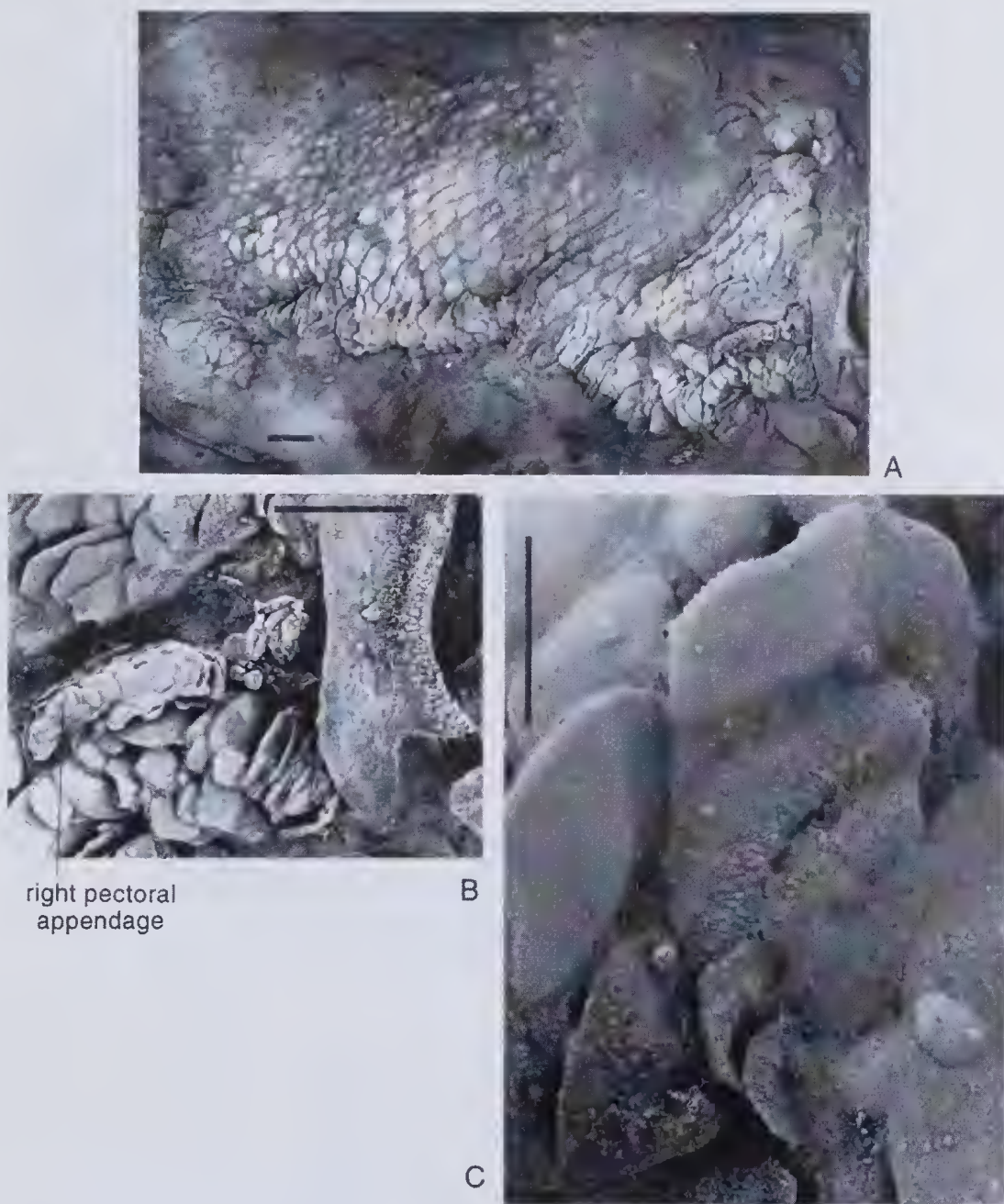


FIG. 11. *Adololopas moyasmithae* gen. et sp. nov. A, body of WAM931.I.221; note the rapid reduction of scale size from front to back and from ventral to dorsal sides. B, cleithrum and right pectoral appendage; note the ornament on the cleithrum. C, enlargement of scales immediately behind the cleithrum; note that the more anterior scales lack cosmine and are covered with pustules. One cosmine-bearing scale in particular has pustules along its posterodorsal edge. Scales A-B = 10mm; C = 5mm.

The lingual face of the juvenile mandibular plates stands almost vertically, and is covered by a sequence of four layers of enamel-covered dentine, the most recently added of them being ven-

tral and the oldest against the plate proper (Fig. 15C,D). In the lingual furrow they have a distinctive shape; their ventral edges are slightly curved except towards the anterior end where they bend

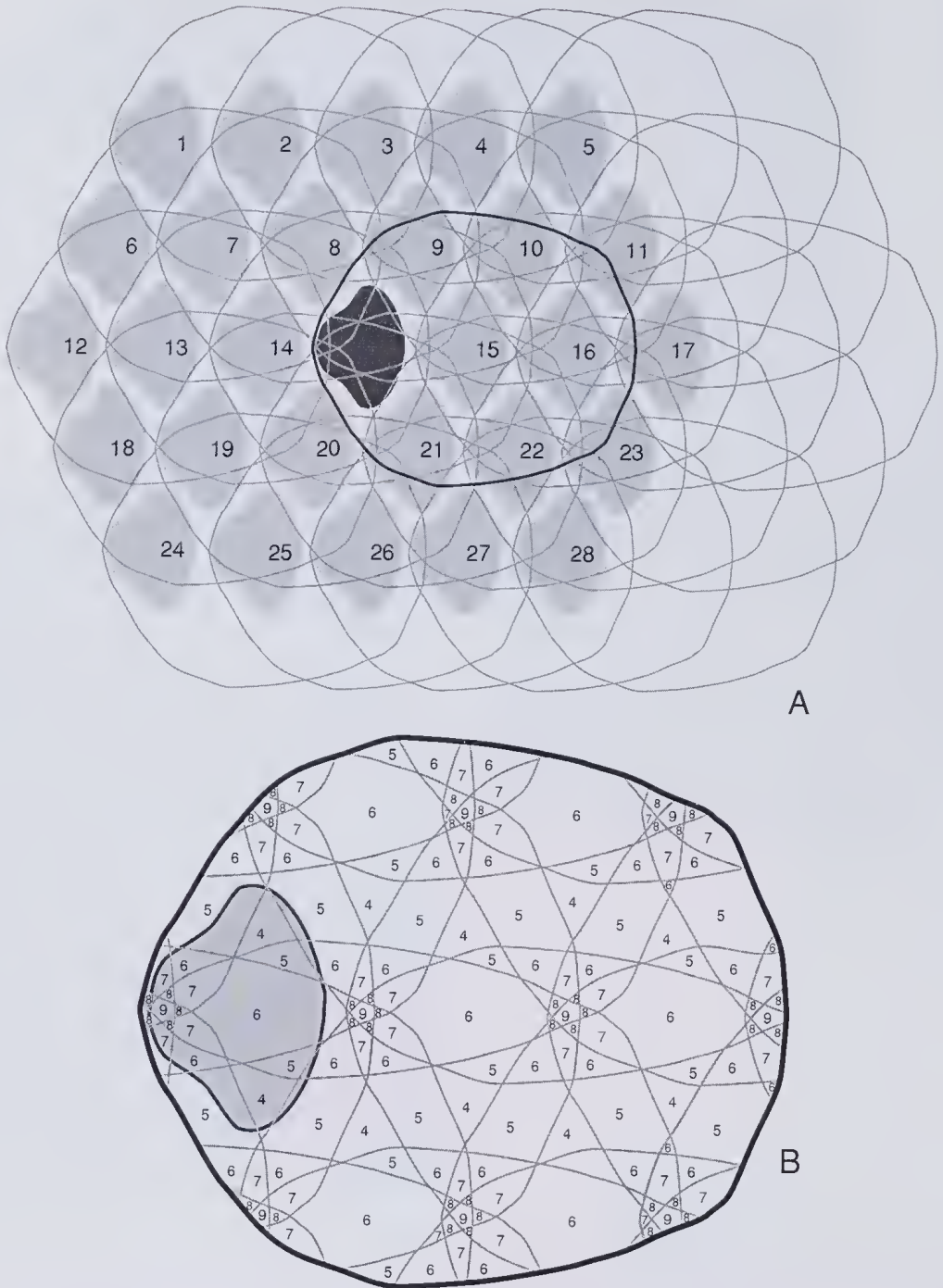


FIG. 12. *Adololopas moyasmithae* gen. et sp. nov. A, computer reconstruction of lateral flank scales drawn on the basis of one scale in dark outline in the centre of the illustration; cosmine coloured black. Cosmine of adjacent scales grey, and surrounded by open areas which indicate bone covered with soft tissue. Twenty eight scales, which potentially were in contact with the main central scale, have been drawn in. B, computer reconstruction of lateral flank scale, cosmine-covered area in light grey, with the estimated pattern of edges of overlapping scales. Numbers refer to the potential number of overlapping scales at particular points on the scale.

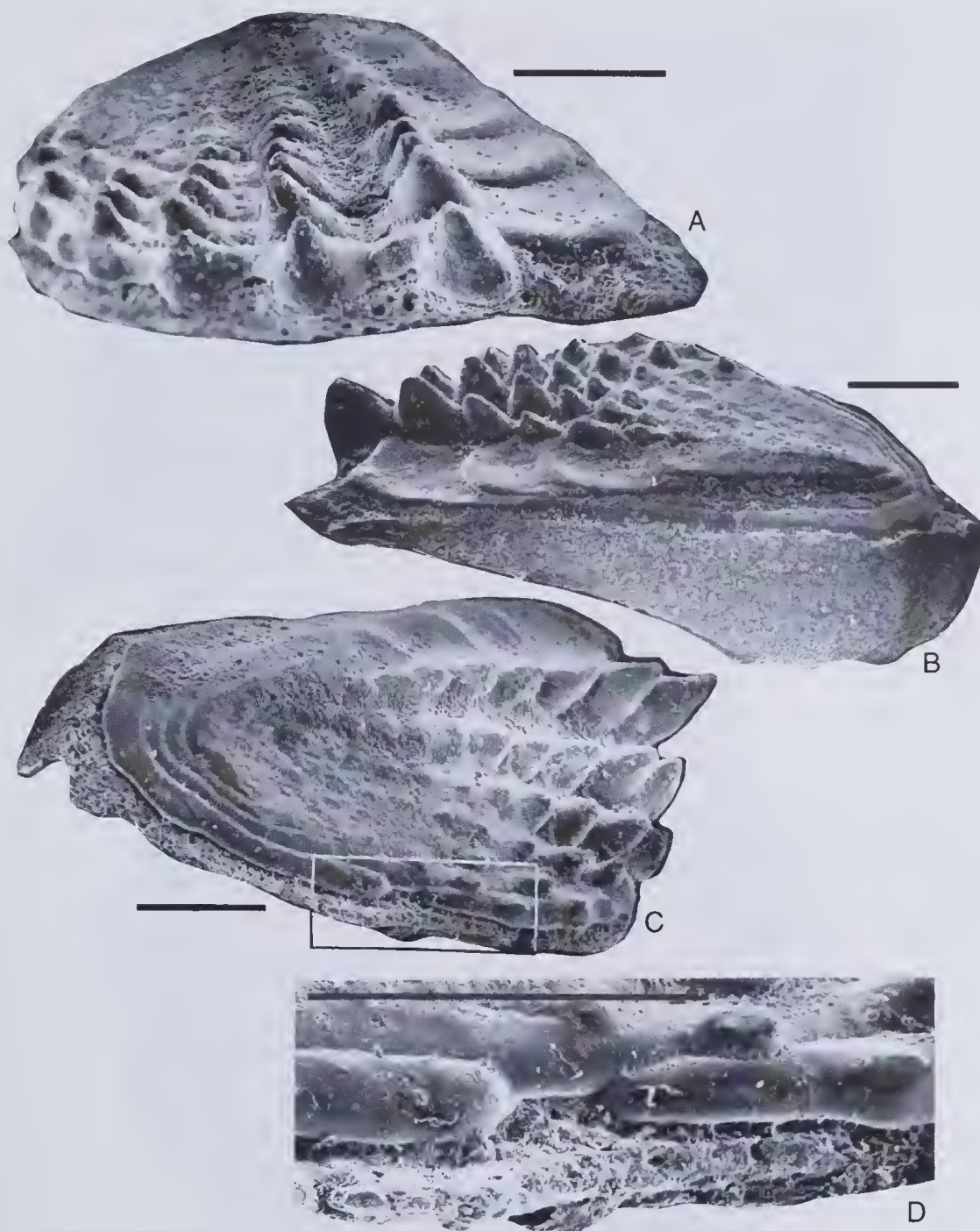


FIG. 13. *Adololopas moyasmithae* gen. et sp. nov. Palatal-tooth plates of the juvenile, ANU49215; right palatal plate (from top to bottom) in anteroventral, medial ventral, ventral and marginal views. A, note the marginal teeth lying directly on bone, and layers of enamel-covered tissue adjacent to the mid-line and bending inwards behind the marginal teeth. B, C, bands of enamel-covered material around the posterior medial and lateral edges, show particularly well. D, shows the break between the posterior band of tissue and the tooth bearing band in front. Scales A-D = 1 mm.

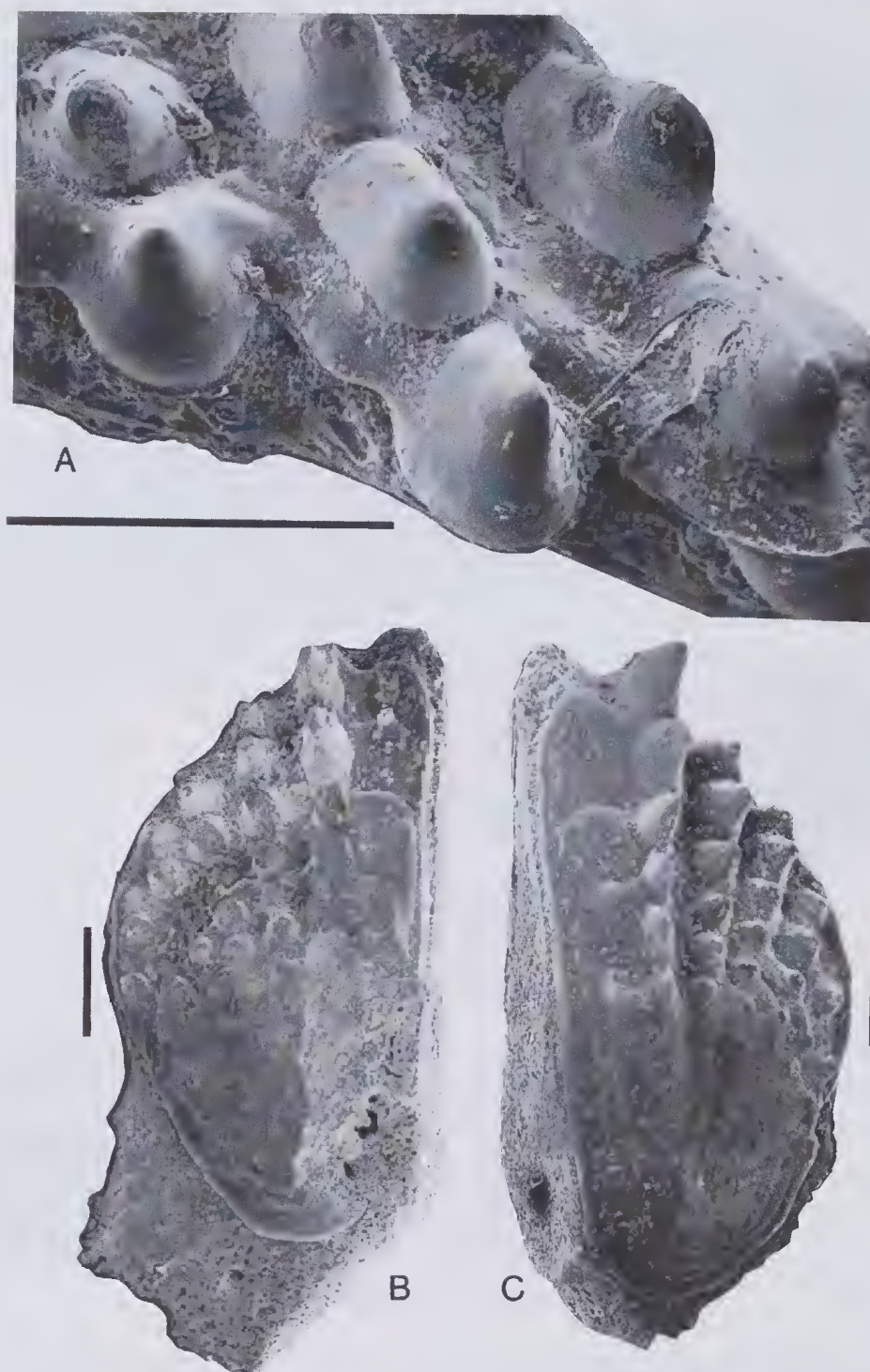


FIG. 14. *Adololopas moyasmithae* gen. et sp. nov. Palatal tooth-plates of the juvenile ANU49215. A, marginal view showing teeth and marginal bone. B, C, two palatal tooth plates of the one specimen. B, slightly destroyed by erosion on the original specimen. Scales = 1mm.

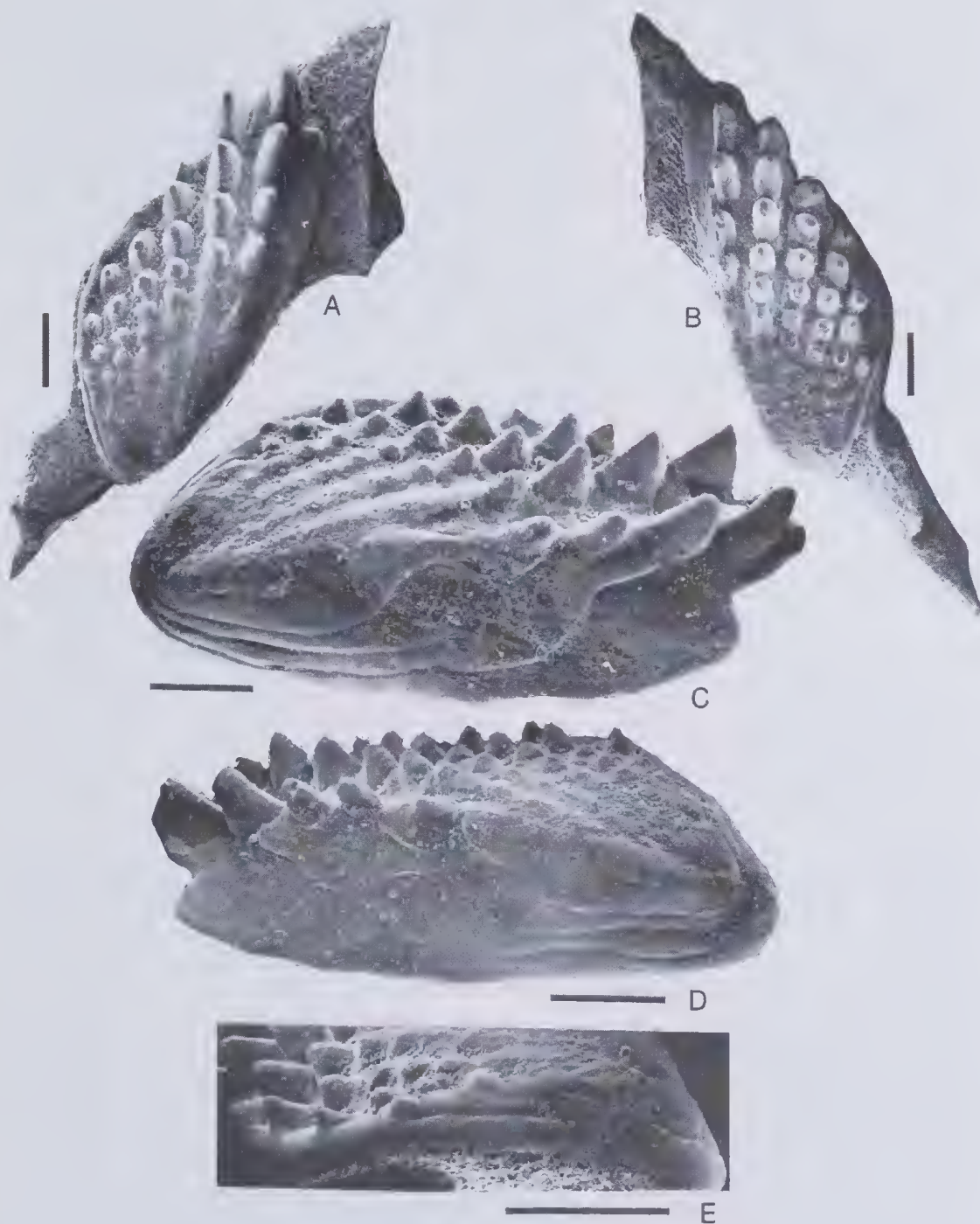


FIG. 15. *Adololopas moyasmithae* gen. et sp. nov. Mandibular tooth-plates of the juvenile ANU49215. A, B, dorsal views of two plates; note the exposed bone in the mid-line. C, D, lingual views of the left and right plates showing the enamel-covered bands. E, view of the posterior lateral edge of A. Scales = 1mm.

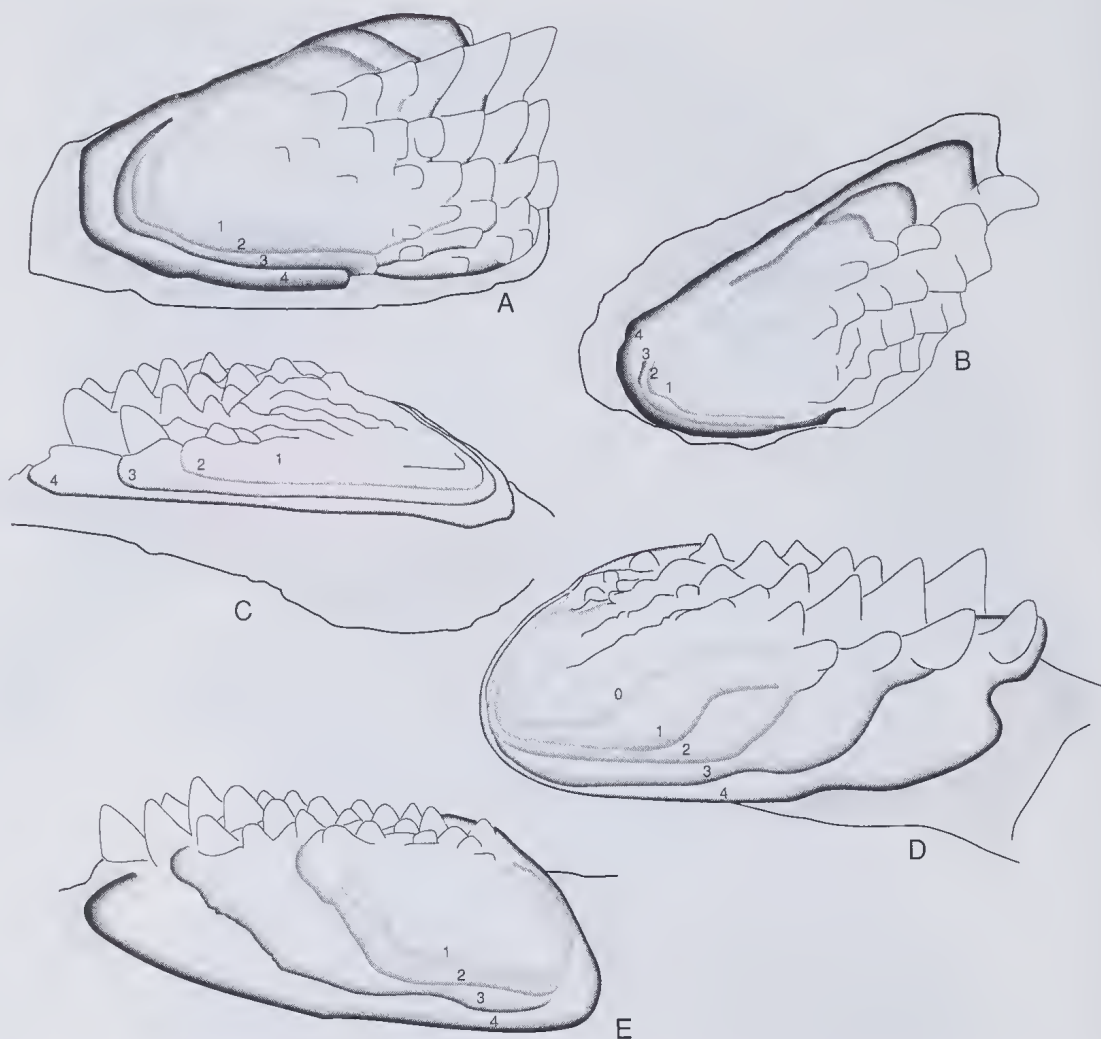


FIG. 16. *Adololopas moyasmithae* gen. et sp. nov. Outline drawings of the juvenile specimens of tooth plates in Figs 13-15. A-C, three views of the left palatal plate showing the marginal bands numbered 1-4. D, E, lingual views of the left and right mandibular plates, again showing the marginal bands 1-4.

sharply upwards and then loop forwards on to the flanks of, or around, the last-formed tooth. This gives the superficial impression that a new layer is formed contemporaneously with the addition of a new tooth, but that is not correct. As is shown by an examination of the anterolateral margin of the plate, new teeth are added directly on to bone and then a layer of dentine was deposited around the distal edges of the teeth. These bands were continued around the posterior margin of the plate, though some of the earlier formed ones were overlapped by the later ones. Only the last formed continues around the lateral edge of the plate, and it turns in behind the distal tooth on the third row and then continues in the furrows proxi-

mal to the distal tooth on the second and first rows.

Macromorphology of Adults. The adult *palatal* tooth plates of two specimens are known. The better preserved one (Figs 4C,D, 17A-D), has 6 well-formed rows of teeth with an indication of a seventh. In ventral view, the posteromedial edge of the plates against the median suture shows the remnants of four dentine bands (Figs 17A, 21). These bands have resorbed posterior edges, and are ingrown to various extents by columns of dark, apparently hypermineralised, dentine. The dark bands appear as slightly darker bands within the white dentine. These bands of tissue narrow anteriorly for about 4mm, where they become

indistinguishable. Anterior to them, the surface of the plate is formed by bony tissue along the median edge of which there are few narrow elongate blisters of dentine which butt up against the mesial side of the two most anterior teeth (Fig. 17D). These blisters become larger anteriorly.

On the posterior margin of both plates three bands of dentine can be distinguished, the inner one strongly ingrown with columns of hypermineralised dentine; the outer one shows an irregular edge, indicating deposition not long before death. This outer band also contains a small number of pores as in *C. australis* (Smith & Campbell, 1987, pl. 4, figs 24-26). The lateral margins of the plate (Figs 17B, 21) have a single narrow band of dentine that continues forward to the fifth or sixth row of teeth where it turns inwards forming a ridge in each furrow proximal to the most distal tooth in each row. This most distal tooth on each row lies directly on bone (Fig. 17B,C), and the concentric layer of enamel-covered tissue abutts the inner edge of the distal teeth, indicating that it did not form a continuous layer around the edge of the plate.

Preparation of the paratype has allowed the dentine to fall free of the pterygoid (Figs 18A,B, 19A,B, 20A-C). A basal pulp cavity is continuous longitudinally beneath the tooth-bearing rows, except at the distal ends where there is bone beneath the outer edge of the last-formed tooth. Bone lies at the distal ends of the teeth and extends slightly beyond it (Fig. 17B,C). Pterygoid bone joins the tooth plate between the tooth rows in thin bands. This bone joins bone and coarse dentine that lies between the rows of teeth on the occlusal surface (Fig. 17B). More detail of this arrangement is described below in the histology section. Along the lateral face of the plate the bone of the pterygoid also makes a continuous junction with the dentine (Fig. 19A). Although the broken specimen is not completely clear, bone also meets the coarse dentine medial to the innermost tooth row. The breadth of this bone increases posteriorly. Beneath the thick solid dentine part of the plate forming the heel, the dentine is braced against the pterygoid by irregular discontinuous masses of bone, which become more closely spaced posteriorly where the dentine thins out (Figs 18-20).

The mandibular tooth-plates are convex, and contain six rows of teeth (Figs 4B, 22B,C); in each row, the last five or six teeth can be distinguished; individual teeth have the same form as those on the palate. The plate is convex, and the most distal tooth lies directly on bone (Figs 10B,

22B,C). The left side of ANU49213 shows the growth series of tooth structure (Fig. 22B). Along the left side of the plate is a continuous layer of enamel-edged tissue which runs forward to, and around, the last formed tooth in the sixth row (Fig. 22B). At that point it turns inwards to form a boundary edge proximal to the distal tooth in the fifth row. It then continues across the plate inside the distal tooth in each row until the median row in which there are two teeth distal to it (Fig. 22B). The bone on which the distal tooth sits is coarse at the base and fines up to the tooth base. As can be seen from the surface, the bone extends inwards between the rows, and becomes progressively more ingrown by dark dentine proximally. Laterally the same type of tissue extends proximally between the sixth row of teeth and the marginal ridge.

A broken mandible (Fig. 22A), shows well the layers of reparative dentine along the lingual surface. These are in short sections in about four layers. Those at the dorsal edge are slightly eroded, and at the ventral edge are fresh, being the latest ones formed. As can be distinguished in this photograph, the bones lie below the dentine and form a slightly concave surface in the lingual furrow.

HISTOLOGY OF ADULT TOOTH-PLATES

DISTAL TOOTH. *Enamel and Pallial Dentine.* The tooth plates add considerably to our understanding of the Late Devonian evolution of the marginal growth mechanisms, the pulp cavities and pulp canals, and the distribution of the various types of dentine. Vertical sections along the tooth rows (Fig. 23A,C) show a continuous basal pulp cavity which extends to the inner edge of the most distal tooth. At that point, the bone runs onto the outer edge of the second last tooth, making a firm connection between the bone and the outer edge of that tooth (Figs 23A,C, 24A,B, 25A,B).

The distal tooth is covered with enamel except on the tritural surface where it has been worn away. The enamel layer extends over the outer surface of the distal tooth terminating deeper than the basal pulp cavity (Figs 24A,B, 25A,B, 26D). Beneath the enamel is a layer of dentine of variable thickness, dark in colour on SEMs, but light in transmitted light (Figs 23A-D, 24A-D, 25A,B, 26A-C,E,F). This is the pallial dentine layer, or mantle dentine of Weidenreich (1925) and Lund et al. (1992), which is found in all Palaeozoic dipnoans. For our usage of pallial dentine, see Campbell & Smith (1987: 166). Some of the pulp canals in the pallial dentine are continuous with

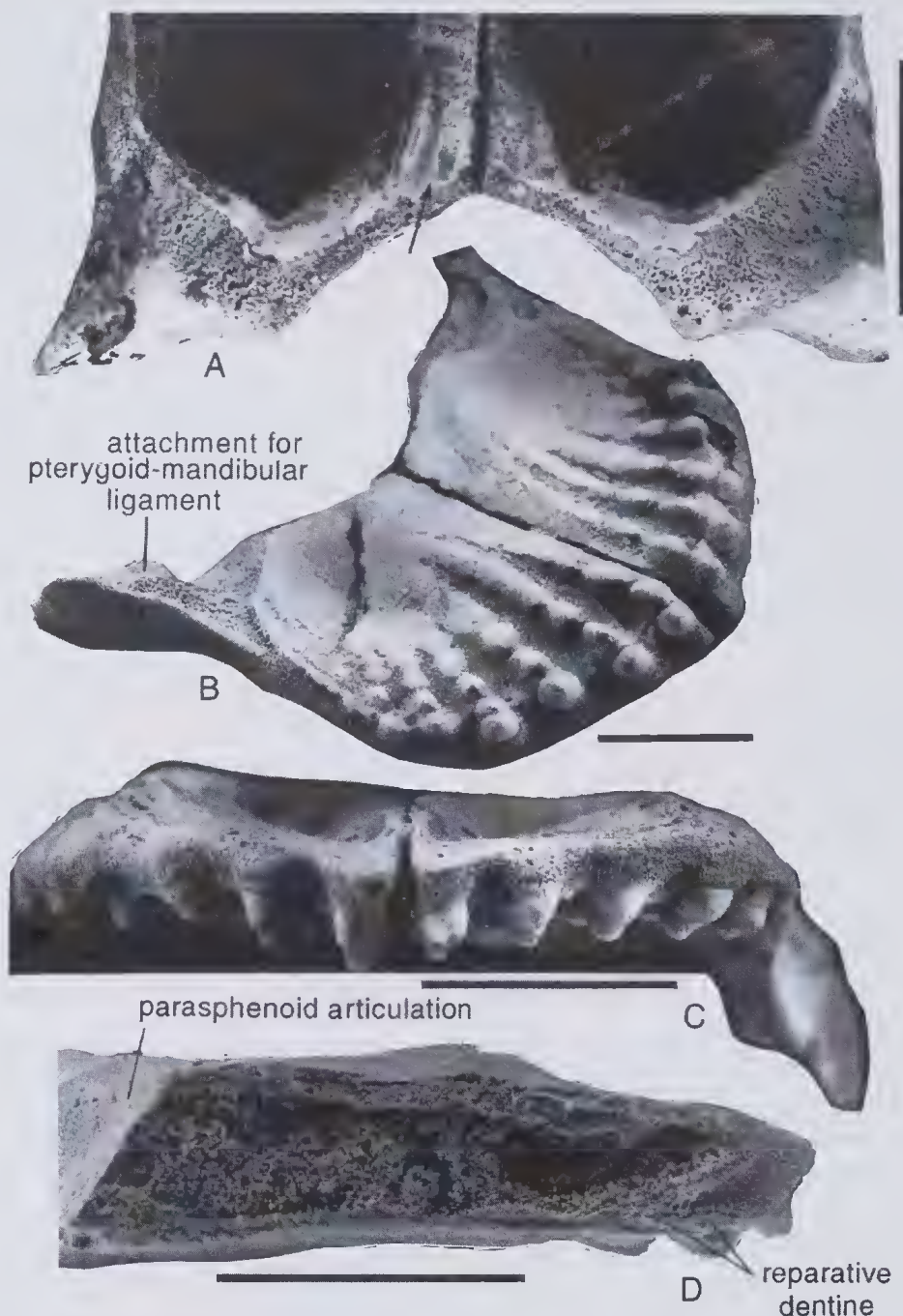


FIG. 17. *Adololopas moyasmithae* gen. et sp. nov. Pterygoid tooth-plates of the holotype. A, view of the posterior part of the palatal plates; note in particular the primitive dentine around the posterior edges of the plates and the successively generated layers of dentine along the median-posterior edges of the plates (arrowed). B, oblique view of the plates. C, anterior end of the same plates showing the teeth lying directly on bone and having enamel forming only around the teeth themselves; note also the down-turned part of the plate to the mandibular articulation. D, medial view of the left tooth plate which has been separated from the other plate; showing the articulation of the parasphenoid and the two small blisters of primitive reparative dentine towards the front of the plate. Scales = 10mm.



FIG. 18. *Adololopas moyasmithae* gen. et sp. nov. An isolated left pterygoid plate of WAM93 I.1.221. A, The dorsal surface of dentine part of the plate showing the bases of the pulp canals. B, bone from which the dentine has been separated; A and B will fit together; B shows the positions of the pulp canals adjacent to the bone, and the white patches are the remains of the bone joining the pterygoid to the dentine plate. Note the abundance of bone attachment under the heel of the plate. Scales = 10mm.



FIG. 19. *Adololopas moyasmithae* gen. et sp. nov. Drawing of Fig. 18, showing the points of contact between the dentine and the pterygoid bone in black. Note that the two surfaces do not fit together because when the two were separated, the bony contacts separated part to one side and part to the other. Fine stipple refers to surface without attachment between the bone and dentine, and coarse stipple to parts of pterygoid not joined to dentine.

those of the core dentine of the tooth, but others are directly connected with the underlying tissue on the inside of the tooth. We refer to this as pedestal dentine, and it will be discussed below (Figs 24A-D, 25A-B, 26C-D). At their tips, the pulp canals in the pallial dentine branch to form a thicket of dentine tubules which are not always obvious (Fig. 26F). Under crossed polarised light, this layer has a different pattern (Figs 24B,D, 25B, 26A) from the remainder of the dentine.

The Core Dentine. In thin section, the core of the distal tooth is made of dark brownish tissue which forms a dense mass. It appears in weathered surfaces as a dark material, and it is hard wearing; so to some extent it must be hypermineralised. In it the pulp canals are slightly bent, but they form continuous structures from the basal pulp cavity to the base of the pallial dentine (Figs 24A-D, 25A,B, 26A,B). The hypermineralised dentine was formed directly from the basal pulp cavity. Occasional branching of the pulp canals is observed, and interconnecting canals are common. Extending out at right angles to the canals are abundant dentine tubules (Figs 24A, 25A, 26D) which are more obvious nearer the pulp cavity, although more occlusally in the tooth they are occasionally visible, where they are narrower.

Tubules are well shown on some SEMs where they are delicate structures which branch repeatedly away from the canal and form a meshwork (Fig. 28B). As is shown in Fig. 27B & C, the crystal fibre bundles composing the dentine make a basket weave throughout the tissue (Smith, 1984), such as occurs in petrodentine. They are similar to the structure described by Campbell & Smith in the teeth of *Holodipterus gogoensis* (Campbell & Smith, 1987). We do not have enough material to cut horizontal sections through each tooth to determine the birefringence of the crystal fibre bundles. The abundance of tubules throughout the tissue indicates that it is not typical petrodentine, though it may be an intermediate stage in the evolution of petrodentine. In fact, it is a compact structure for which we can find no acceptable term among the many available ones. We will therefore refer to it as 'a compact dentine' in generic terms, not intending that this be taken as a new term for dentine morphology.

Pedestal Dentine. Between the pallial dentine and the compact dentine of the distal tooth, is a layer of dentine which has pulp canals which are very



FIG. 20. *Adololopas moyasmithae* gen. et sp. nov. A, occlusal view of pterygoid tooth-plate. B, dorsal view of tooth-plate, but reversed so that it is in the same orientation as the occlusal view, to show the alignment of the bony patches of the underside of the tooth plate as they correspond to the gaps between the surface ridges. C, bone of the pterygoid to show the surfaces to which the dentine plate was attached. Arrows indicate points of the superimposition of dentine on bone. Note that B is a mirror image of the underside of A, and it represents the joining surface with C. Arrows indicate the points of superimposition.

distinct in some sections and weaker in others. This dentine is well shown in Figs 24A,C, 25A,B, 26A-D. It has the same colour as the underlying bone. It is always better developed on the inner edge of the distal tooth than the outer. The pulp canals in this dentine do not connect with the basal pulp cavity at their bases, but towards the occlusal edge of the tooth they are connected into the pallial dentine (Figs 24A, 25A, 26B-D). At the base they seem to grade into bone, which is distinguished by osteocyte spaces. Dentine tubules, coming off pulp canals, are not obvious in this dentine, but occasionally they can be detected. In Figs 24A,C, 26A-C this dentine is in contact with the core dentine of the previous tooth, and cuts into the dentine pulp canals of that tooth. As seen in Figs 23A,C, 26A-C, this dentine is lost, presumably by resorption, and it is not visible in any preceding tooth.

Some pulp canals extend into the tissue between the distal tooth and the preceding tooth (Figs 23A,B, 24A-D, 26A-C). As can be seen in Figs 24A-D, 26C, which are optical photographs, and Figs 23A-B, which represents the SEM reproduction of the same feature, this layer of the most distal tooth lies occlusal to the enamel and pallial dentine of the second last tooth. The enamel (Fig. 23B, 24A-D) is left embedded in the matrix and it surmounts the bone on which it lies. The sharp boundary between this layer, and the underlying compact dentine which forms the core of the tooth, is well shown on Figs 23B, 26C. The SEM shows how the compact dentine does

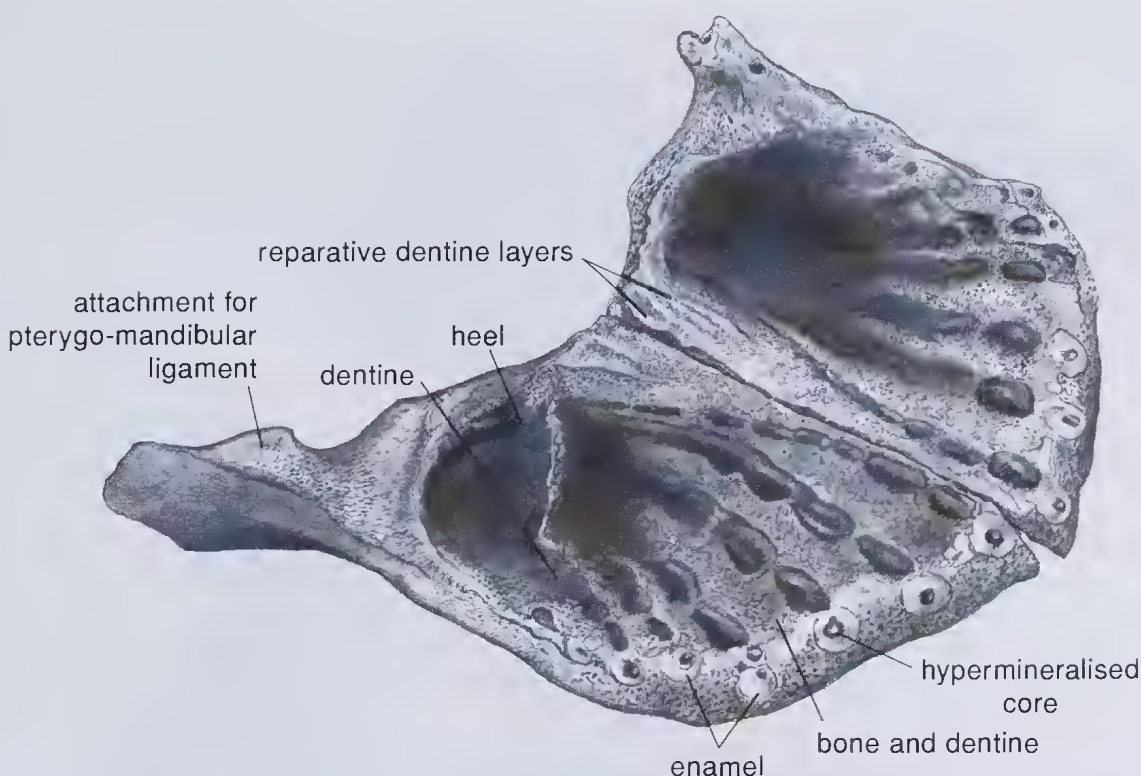


FIG. 21. *Adololopas moyasmithae* gen. et sp. nov. Oblique view of pterygoid plates of the holotype showing up the detail of bone, dentine and reparative dentine. Compare Figure 17B. Note particularly the presence of white tissue representing the enamel-covered surface around the teeth and forming a layer on top of bone between the distal teeth.

not etch as easily as the outer dentine layers.

The naming of this dentine is important. It is not interdenteonal in origin, it has poorly developed tubules, and occlusally it merges with pallial dentine, but at the opposite end it grades into bone with no distinct boundaries. The function of this dentine is to provide an outline on which the distal tooth was deposited. We consider that it should be called 'pedestal dentine' (Smith, 1985: 629). Pedestal dentine is a primary dentine joining pallial dentine to the bone of attachment.

MORE PROXIMAL TEETH. The second and third teeth from the outer edge of the plate have most characters in common with the last tooth. The second tooth overlaps the third tooth directly; most of this contact takes place between the compact dentine of the teeth, but towards the occlusal surface the pallial dentine of the two teeth are in contact (Fig. 23A,C). No sign of the pedestal dentine as described in the distal teeth can be seen in these older teeth. Presumably it was there originally, but it has been resorbed to allow other dentine to develop in its place. The initiation of

this resorption is visible in the pulp cavity (Fig. 23A,C). The compact dentines of the second and third teeth are contiguous, and in some places the only way of distinguishing them is the fact that the canals diverge slightly at the junction. The pulp canals tend to be long and relatively straight, but they are interconnected irregularly (Fig. 24C-E).

The fourth and more proximal teeth become less prominent as a result of wear (Figs 17B, 21). They are composed of continuous core (compact) dentine, but with a relict of pallial dentine in some places.

Against the basal pulp cavity, it is possible to distinguish the base of the dentine columns in the core of the teeth (Fig. 24E-G). These ends are rounded in vertical section, an indication that there was continuous deposition around them by a layer of cells. The dentine formed in these positions has the same internal structure and colouring as the dentine higher up in the tooth; the only real difference is that the dentine has less obvious tubules away from the basal pulp cavity.

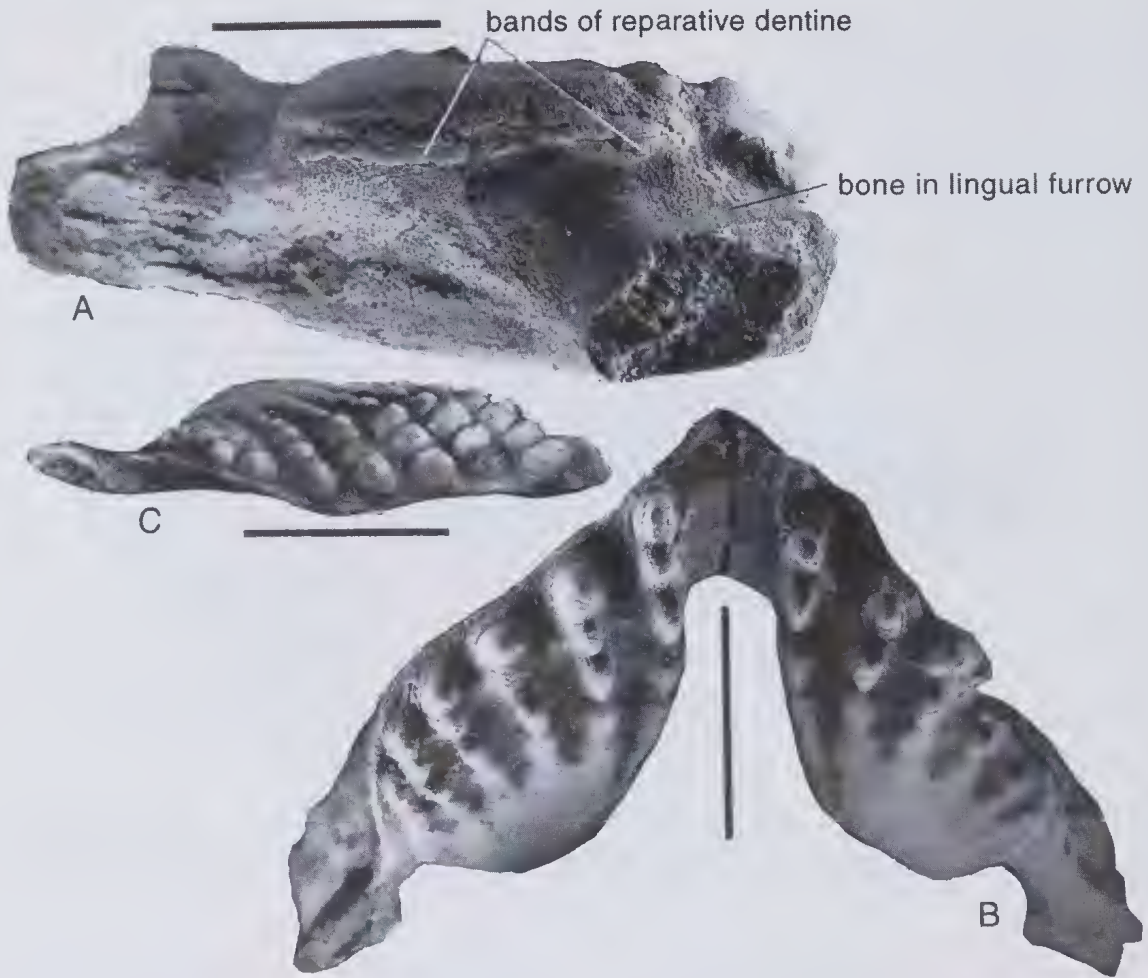


FIG. 22. *Adololopas moyasmithae* gen. et sp. nov. A, lingual view of the mandible of the holotype, with the right side of mandible removed; note the bone in the lingual furrow and the bands of reparative dentine along the basal edge of the dentine of the plate, with solid dentine dorsal to it. B, dorsal view of same with the two parts together; the specimen is tilted with the anterior upwards to show the anterior teeth against the bone. C, lateral view of WAM931.1.221 to show the curvature of the plate. Scales = 10mm.

Dentine tubules are abundant close to the basal pulp cavity (Fig. 24E-G). Although the pulp canals thin out towards the occlusal surface, we have been unable to distinguish any clear evidence of intratubular or peritubular dentine (Baume, 1980). There could be two possible causes — the thickness of the sections studied which cover up the boundaries of such layers, or to the fact that no such deposits are present, and the the pulp canals become wider towards the basal pulp cavity.

We have not had sufficient material to cut horizontal sections of a tooth to observe the pattern of extinction under crossed polars such as occur in petrodentine. SEMs also show the fibre bundles in this dentine clearly, as on the right and left sides

of Fig. 27B. The following features are also inconsistent with the dentine being petrodentine (Smith, 1984); dentine tubules are present widely through the tissue — these are visible in both thin sections and in SEMs; the whole dentine is stained brown, whereas petrodentine is clear; and, the dentine is made up of tissue laid down at the base of each column (Fig. 23E-G), and is devoid of tissue that could be interpreted as having been laid down from a special layer of petroblasts.

An isolated tooth-plate of WAM931.1.221 (Fig. 18), from which the dentine has been separated from the pterygoid bone, has been cut in an oblique transverse section about two teeth in from the margin. The section has been subjected to SEM examination (Figs 27-29), and the adjacent

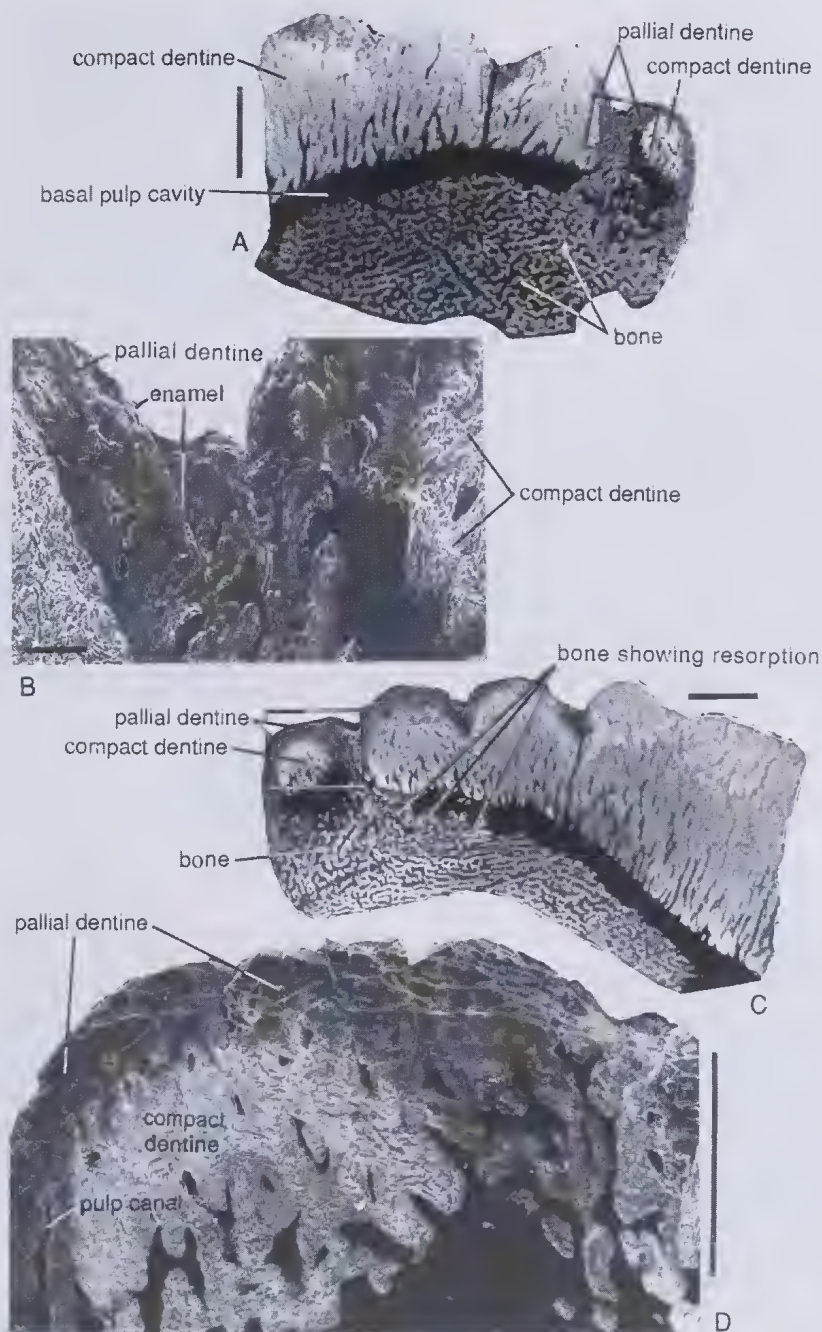


FIG. 23. *Adololopas moyasmithae* gen. et sp. nov. A, C, SEMs of two sections cut from a tooth row from WAM931.1.221; note the early initiation of compact dentine in the last formed tooth surrounded by a mass of dentine supported at its base by bone and dentine which extend up from the basal pulp cavity. This outer layer is lost on much of the second teeth. Note also the large open space of the basal pulp cavity below the tooth row, and the structure of the supporting bone. B, enlargement of the junction of the last two teeth on A, as outlined on A. The enamel which extends down into the tissue is labelled; the junction between the two layers of compact dentine and the surrounding tissue is obvious. D, enlargement of the distal tooth of C; on the right side note how the pedestal dentine extends up around the compact dentine. Scales A, C = 1mm, B = 0.1mm, D = 0.5mm.

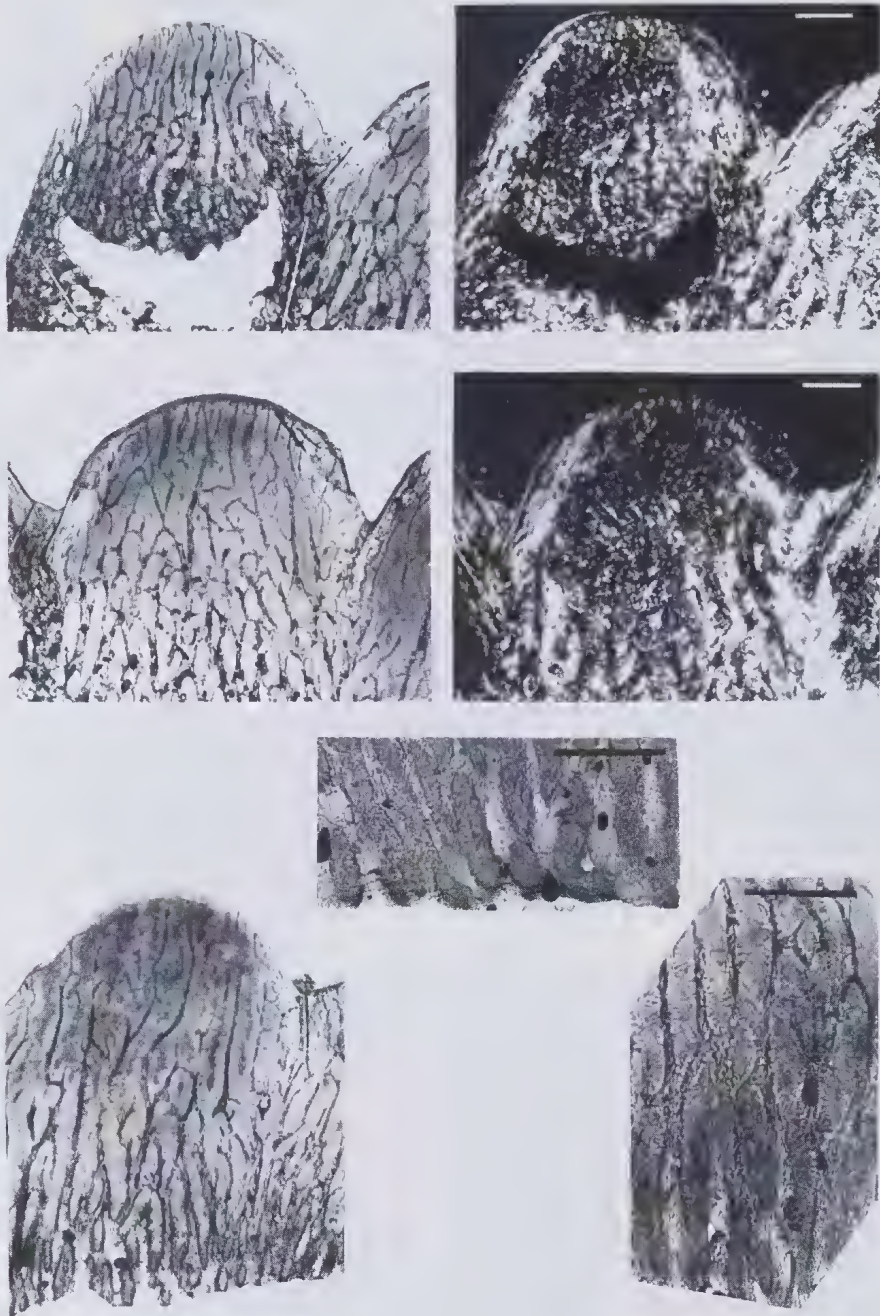


FIG. 24. *Adololopas moyasmithae* gen. et sp. nov. A, B, optical thin sections of the most distal tooth shown in an adjacent section in Fig. 23B; A is in plane polarised light and B in crossed polarised light. This shows the bone and the pedestal dentine extending up into the base of the tooth. C, D, the second tooth along the tooth row; C is in plane polarised light and D in crossed polarised light. Note the absence of pedestal dentine built into the tooth on the right side. E, an even more proximal tooth showing the basal pulp cavity at the base, and the long regular pulp canals which divide more extensively at the base than at the top of the tooth. F, G, two sections from the base of teeth to show the pulp canals running from the basal pulp canal, and also a number of dentine tubules extending into the tissue. Scales A-E = 0.25mm; F-G = 0.3mm.

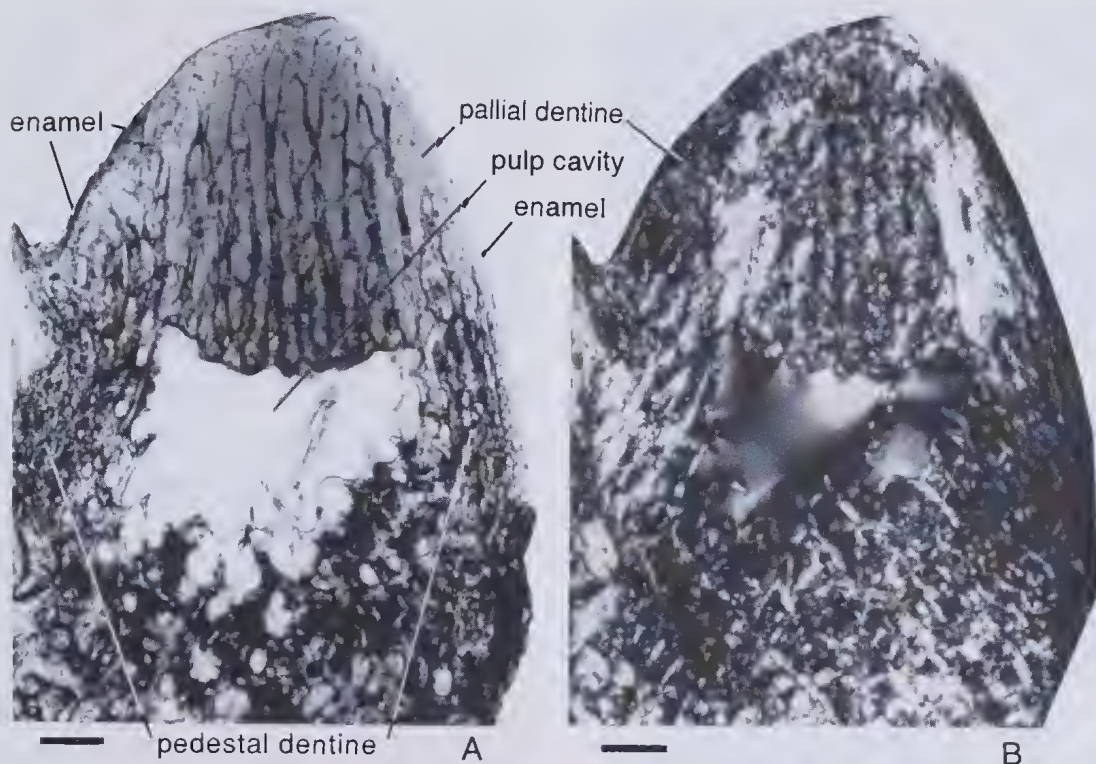
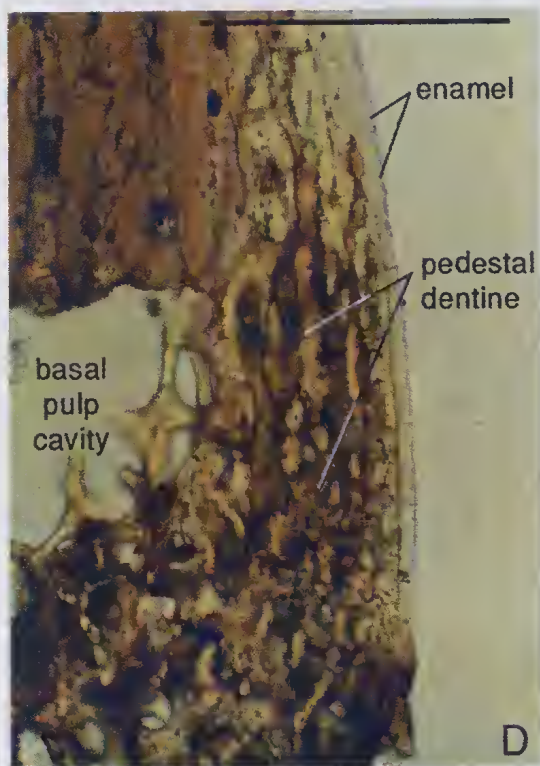
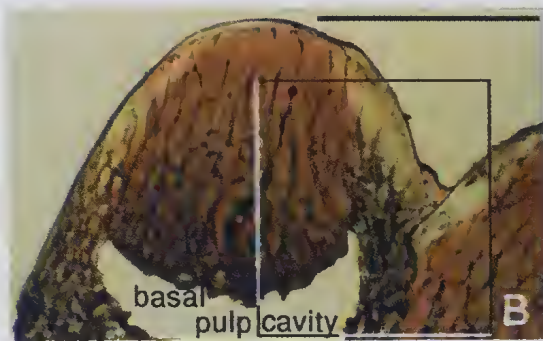
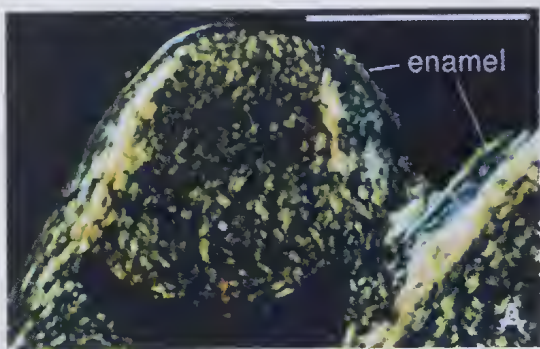


FIG. 25. *Adololopas moyasmithae* gen. et sp. nov. Optical photograph of the distal tooth of a second cut through WAM931.1.221. A, under single polarised light; B, under crossed polarised light. This specimen shows in better detail the bone and pedestal dentine as in Fig. 23. Scales = 0.25mm.

parallel section has been cut for work on the optical microscope. These sections show much detail of the tissue in the valleys between the tooth rows and its relationship to the basal pulp cavity. As indicated above, the valleys between the tooth rows are filled with what appears to be coarse dentine in natural light. Across this whole section (Figs 27A, 28A, 29), some of this inter-tooth-row dentine lies at the occlusal surface of the plate. The contact with the adjacent tissue of a tooth (compact dentine) is sharp, and there is no evidence of intergrowth of the intervening pallial dentine by pulp canals turned laterally from the pedestal dentine. The dentine in these valleys is formed of bands of tissue around pulp canals (Figs 27B,C, 28A, 29), and these bands are made of tissue like the compact dentine cores of the teeth. Many of the pulp canals are turned parallel with the occlusal surface, but deeper in the tissue the canals join and form a more continuous layer. The boundary between the filling tissue and the underlying core tissue is shown in Figs 28A, 29.

The space between the last and second last tooth on the right in Fig. 27A is shown in detail in Fig. 27B-C. It shows the fine structure more clearly

than elsewhere on the section because it is the most recently formed unit between the tooth rows, and it lies over a patch where the tooth-plate surface is supported to the pterygoid bone as described above. This SEM shows no fine structure between the masses of dentine in the inter-tooth-rows, but some fine tissue must have been present in the original. Such material appears on the untreated specimen as whitish substance lying between the darker dentine columns (Fig. 17B). Thin sections of this material (Fig. 30) show that it is composed of bone which does not show up well on SEMs. Figure 27B,C are also important because at the base of the column the remnants of pterygoid bone supporting the dentine, are seen. This bone represents the hard columns of bone which appear in Figs 18-19 between the open spaces below the radial tooth rows. Fig. 27 B,C shows a slight enlargement in which the dentine in the canals meet the bone, and shows the way in which the bone is surrounded by dentine growing over its surface away from the pulp cavity. In part, this provides an understanding of why the canals in the inter-tooth rows are oblique to the rows in the teeth, and it also shows the similarity in struc-



ture between the dentine in the tooth cores and the inter-tooth-row spaces. It also demonstrates why the boundary between the inter-tooth dentine makes a sharp boundary with the tooth dentine.

Figure 28A shows the third tooth from the right in Fig. 27A, together with the tissue occupying the inter-tooth-row spaces. Because of the obliquity of the section in Fig. 27A, Fig. 28A is an older tooth than the one shown on the right side of Fig. 27A. Note the hard white compact dentine in the core of the tooth and the darkish layer on each side. An enlargement of the inter-tooth-row (Fig. 29) shows the sharp contact between the tooth dentine and the darker tissue between the tooth rows. The dentine in the inter-tooth valleys consists of largely globular masses separated by light coloured substances, as mentioned above. As can be seen from the growing edge of a plate, bone occupies the spaces between the tooth rows (Figs 17B, 21). With increasing age, dentine is deposited from pulp canals which grow up into the bone, with bone lying between dentine. Finally, the heel of the dentine plate is formed by the exclusion of bone, so that the heel is made entirely of compact dentine.

Figure 30 shows stages of the development of this dentine. Bone, with the osteocyte spaces clearly preserved, is shown surrounded by dentine and its pulp canals. The newly formed dentine beginning to occupy the spaces between the bone is shown on Fig 27B, C. The dentine which forms in the valleys between the tooth rows is of the same type as the hypermineralised dentine (compact dentine) that forms the cores of the teeth.

This new genus shows an intermediate stage in the development of a continuous pulp cavity beneath the dentine, as is shown in Mesozoic and later species. The dental plate in *Adololopas* is still firmly attached to the pterygoid or the prearticular at numerous points (Figs 18, 19, 20). It still retains some bone and intergrowing dentine in the valleys between the tooth rows. Evolution in later lungfish reduced the bone, and the dentine of adjacent tooth rows joined up laterally to make a continuous layer of dentine across the plate. Of course, associated with this change are the

changes in dentine structure which have been described by many authors such as Denison (1974) and Smith (1984).

REMARKS. The arrangement of the bones making up the posterior part of the skull roof is problematical, but enough is known to make the distinctiveness of the roof apparent. The posterolateral edge of I carries an articulating groove indicating either that Z fitted around the corner of that bone, or a loose Y_2 was present. The shape of the operculum with its intumed dorsal edge is of great value in determining the presence of bones on the posterior part of the skull. Although Y_2 and Z were not preserved, it is possible to show that they were present originally because the operculum fits neatly against the bone 8 and turns inwards against the Y_2 and Z. On this reconstruction it becomes apparent that the genus was completely different from *Jarvikia* and *Gnathorhiza*.

A further complication is that the canal running forwards from I apparently enters a large bone which is situated too far posteriorly to be an X, and can only be a modified Y_1 . Judging from the embayments in the flanks of J, and from the position of the canal exiting anterolaterally from J into what normally is K, X must have had a relatively small contact with J, but the shape of its contact with 3 shows that it expanded laterally; K had a large contact with J (Fig. 1), and its anterior outline remains unknown. The position of K relative to X and L is a matter of importance. In *Dipterus valenciennesi*, K is a small bone between X and L; but with the increased size of K and the anterior position of X in *Adololopas*, L is further forward also. Unfortunately we do not have an X or a K to check if a lateral line canal joins the two bones.

Too few specimens are known to permit a discussion of the variability of the species except for one point—the ornament on the pectoral girdle. On WAM931.1.221 the anterior edge carries closely spaced pustules, but these are not present on ANU49213. Other features of both cleithrum and clavicle are closely comparable.

Comparison should be made with the tooth plates of *Scaumenacia curta* Whiteaves, the best

FIG. 26. *Adololopas moyasmithae* gen. et sp. nov. A, B, distal tooth as illustrated in Fig. 24A, B, emphasising details of dentine structure; A, is in crossed polarised light. C, an enlargement of B to show details of the tissue containing pulp canals but lying outside the enamel of both the teeth. Note also the resorption of the second last tooth, now occupied by pedestal dentine of the distal tooth. D, enlargement of the edge of the distal tooth shown in Fig. 25A; note the thick enamel layer, the pedestal dentine and the bone beneath it. E, contact between the distal tooth and the preceeding one, showing pallial dentine in both, but with the dentine tubules difficult to observe. F, contact between the second and third last teeth, showing the dentine tubules in the pallial dentine and the abundant tubules in the adjacent compact dentine. Scales A, B = 1 mm; B = 0.25 mm; D-F = 0.5 mm.

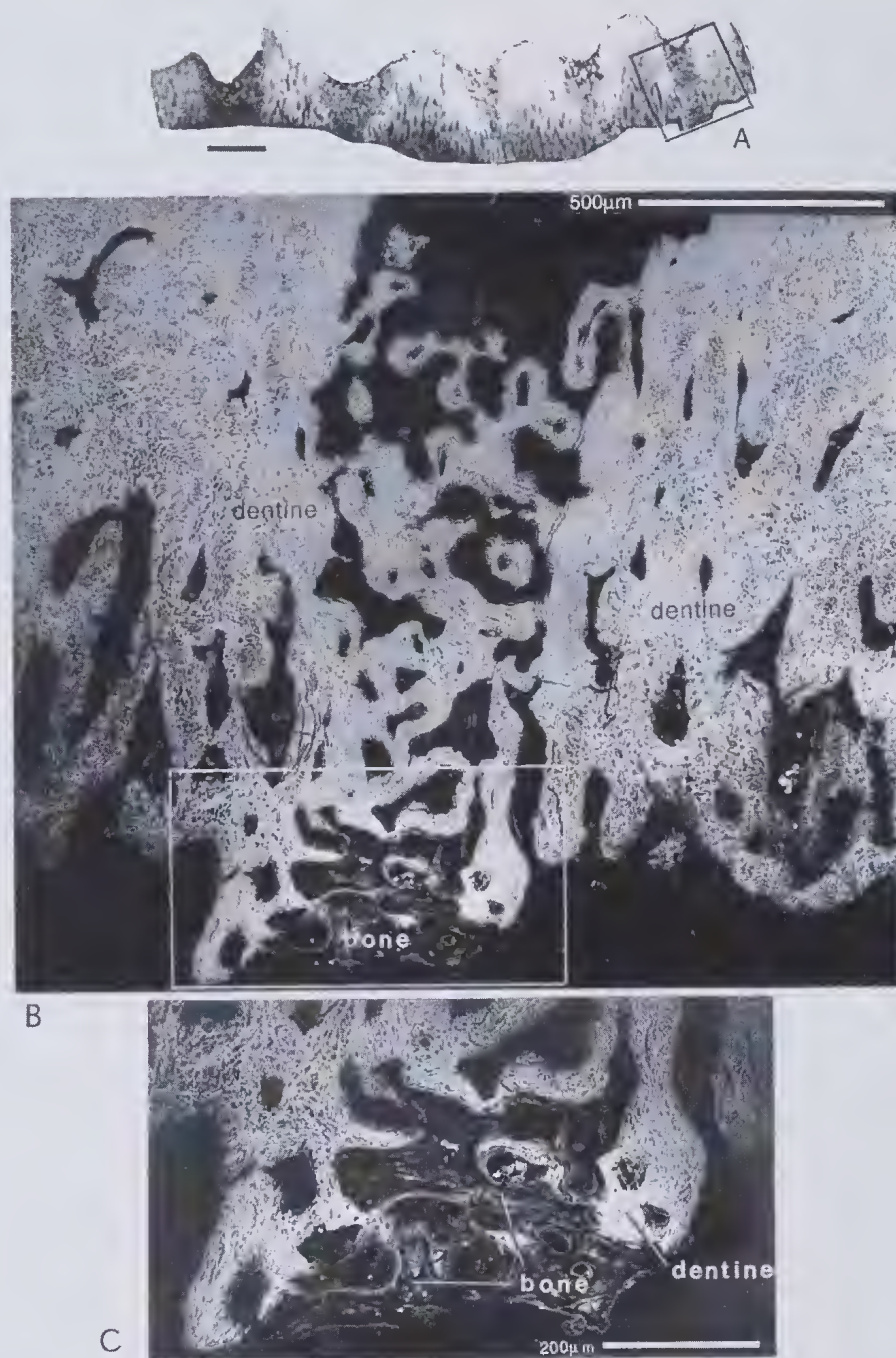


FIG. 27. *Adololopas moyasmithae* gen. et sp. nov. A, SEM of transverse section across the anterior part of WAM931.1.221 showing the teeth and the dentine filling the inter-tooth-row spaces. B, section through the last inter-tooth-row space outlined on the right of A showing the texture of the dentine in the teeth and the orientation of the pulp canals. A small amount of bone lies at the base of the dentine. C, an enlargement of the space outlined on the basal part of B showing the dentine-bone contact, and the formation of the new dentine around the bone spaces. Scale A = 10mm.



FIG. 28. *Adololopas moyasmithae* gen. et sp. nov. A, third tooth from the right in Fig. 27A and the infillings of the inter-tooth-row valleys. B, dentine close to the base of a pulp canal adjacent to the basal pulp cavity; note the branching nature of the dentine tubules.

known of the Frasnian genera from elsewhere in the world. These have been described by Denison (1974), Smith et al. (1987), and Cloutier (1996). Denison thought that the plates of *S. curta* had grown in the same way as those of *D. valenciennesi*, but their histology was entirely different. Unlike *D. valenciennesi*, the specimen of *S. curta* sectioned by Denison (refigured here as Fig. 32E, F) had well-differentiated dentine and bone, separated by small resorption pulp cavities at the base of at least the most labial tooth; and the dentine canals, though branched, were much more regular than those of *D. valenciennesi*. Denison claimed to have observed a small patch of pleromic dentine in the most proximal of the teeth in the section figured, but not in any of the others. We have examined the specimen and have been able to



FIG. 29. *Adololopas moyasmithae* gen. et sp. nov. Enlargement of the space to the left of the third tooth from the right in Fig. 27A showing the contact (arrowed) between the compact dentine of the tooth core and that of the space between the teeth. Note the black gaps between the dentine that seem to have no tissue in them. They are filled with thin bone which does not show up on SEMs, but is well shown in optical thin sections (Fig. 30). Scale = 0.5mm.

confirm most of the points of Denison's description, although the mounting medium has crystallised, destroying the clarity of much of the slide. We have found a small patch of what Denison refers to as pleromic dentine, but we do not consider that it has any importance. Smith et al. (1987) have given a more complete account of *S. curta*, and have added more histological information.

Cloutier (1996) has figured palatal plates of *S. curta* which show clearly the suture between the two plates, the elongated lingual row on each plate, and the extension of the tooth rows to the heel of the tooth. In addition, his specimen is recorded as having 'small tubercles of enamel infrequently added posteriorly and posterome-

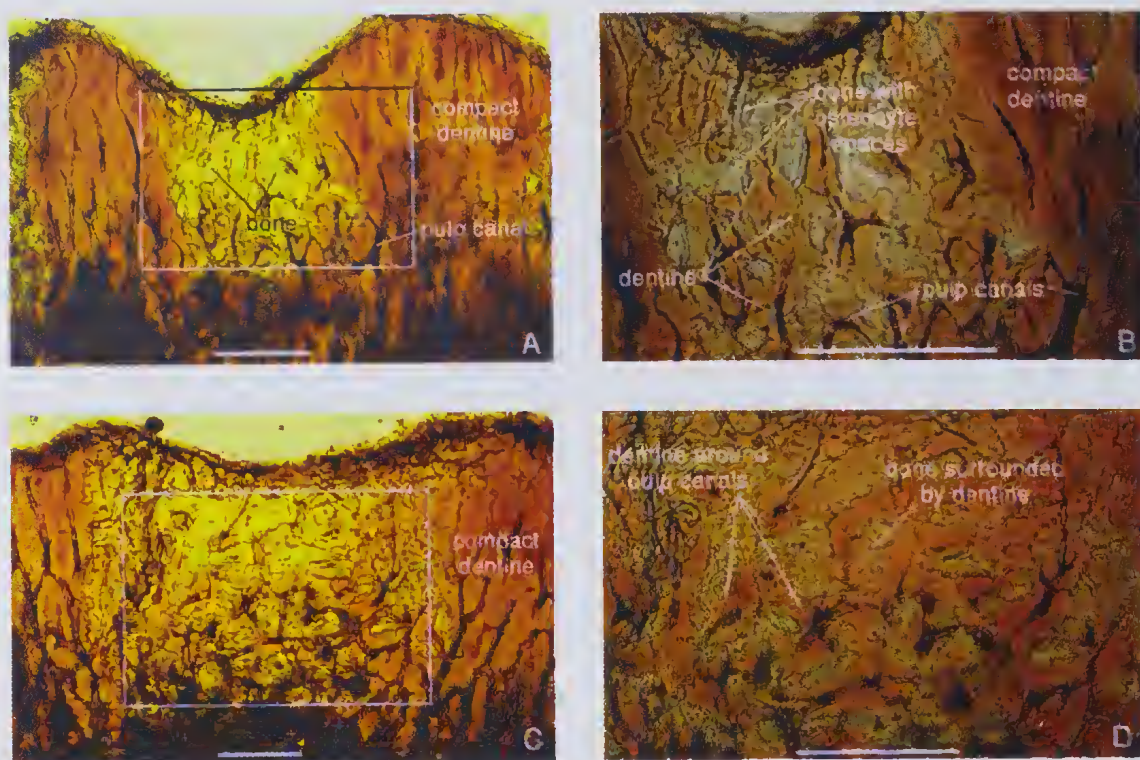


FIG. 30. *Adololopas moyasmithae* gen. et sp. nov. Optical sections cut parallel with the section in Fig. 27A. A, B, a section in which the amount of dentine is only partly developed; C, D, a section in which the bone is more extensive. B and D are enlarged areas of A and C respectively. In A and C the pulp canals are surrounded by compact dentine, the dentine of adjacent canals being in contact. In D the pulp canals are not so common, and places where bone is surrounded by dentine to form a core, are well shown. Osteocyte spaces are present in the bone. Scale = 1mm.

dially to repair the heel of the tooth plate', and he comments that there is a thin layer of enamel covering most of the surface of the tooth plate. The first point indicates that the primitive pattern of denticles is maintained in this genus. The second point is difficult to accept because enamel is laid down as a tissue on the outer surface of a tooth, and should not be present in the intervening furrows between the tooth rows, unless the adjacent tooth rows converge. Such does not seem to be the case. We also note that Cloutier's fig. 6, seems to show a broad band of exposed bone mesial to the lingual row of teeth, but Smith et al. (1987, p. 315) comment that there are simple sheets of dentine in that region. In addition, they note that there is no bounding layer of enamel around the outer margins of the teeth. It seems that in these respects *S. curta* is closer to *Adololopas* than to later genera.

We have been able to cut thin sections of two small topotypic tooth-plates of *Scaumenacia curta* given to KSWC by Denison. Both oblique transverse and vertical sections are available, one

of the vertical sections being of the most labial tooth in a row. All sections show the usual enamel layer over a layer of pallial dentine. Low down on the tooth, ventral to the pallial dentine, is a coarse open tissue, as in *Adololopas*. This tissue is continued downwards into the bone, and its detail is like that of the bone, (though without osteocyte spaces). We therefore refer to it as pedestal dentine as in *Adololopas*. It is heavily stained with iron compounds, and the internal structure in some places is difficult to determine. On the other hand, it is possible to recognise dentine canals extending into it from the more medial part of the tooth (Fig. 32A, B). The core of the tooth is composed of hypermineralised dentine (referred to by Denison (1974) as trabecular dentine, and by Smith et al., 1987, as petrodentine) that has minimal iron-staining, and shows pulp canals like those figured by Denison (1974, fig. 5), i.e., they are essentially vertical but divide and rejoin to form a coarse reticulum. It is possible to recognise a few small dentine tubules extending from the dentine canals into this tissue, but the tubules are



FIG. 31. Lateral view of a head of *Chirodipterus australis* Miles. Note the shape of the lip outline which has been dotted in where bone is missing. Scale = 10mm.

irregular in their distribution and they are much shorter and narrower than those in ordinary dentine. In cross-polarised light, the cross pattern reported by Smith in petrodentine has been observed.

In a section along a tooth row (Fig. 32E,F) the column of petrodentine extends almost up to the crest of the tooth, demonstrating that its deposition began shortly after the trabecular dentine was formed in that region. In teeth that have completed growing, the petrodentine lies directly on the basal bone. In more recently formed teeth there is a basal pulp cavity which is small and gives a space into which the petrodentine grows. This basal pulp cavity is small in the most recently added tooth in Denison's specimen (Denison 1974, fig. 5A,B). In the ANU specimen it is large and has a clear opening into which growth may occur. In more proximal teeth, no basal pulp cavity is present. Presumably it has been filled by downwardly growing petrodentine. This is unlike the situation in *Adololopas*, in which the basal pulp cavities remain open under a number of teeth and into the more solid proximal parts of the plates.

DISCUSSION OF LONG HEADEDNESS IN DIPNOANS

Schultze (1992) pointed out that some Devonian dipnoans are long-headed because of the length of the snouts and others because of the length of the posterior parts of the heads. This analysis makes many useful points, but it has some difficulties which we will discuss here be-

cause *Adololopas* has a long cheek and should fall into the second of Schultze's categories. In our view the length of the head is related to a number of functional factors including gathering food, reduction of food, and the position of the gill chambers.

The first problem to us is one of misinterpretation of data; e.g., the reconstruction of the snout of *Uranolophus wyomingensis* (Schultze, 1992, fig. 5C). In our view, he shows the eye placed too far forward. This position is not explained in his text, but quite clearly the elongate bone lateral to L₁ on Schultze's fig. 5C should be a bone 3, and the eye should be placed ventral to it. His value of l^d for this species is incor-

rect. What is more, the posterior part of the head is more elongated than it should be in relation to the snout with which it is figured, a point that is illustrated by a comparison of the figures of Denison (1968, fig. 3A) and Campbell & Barwick (1988b, fig. 2C). With the eye put into its correct position, this genus shows a greater comparison in skull outline to the adjacent figure of *Soederberghia groenlandica* in Schultze's paper.

Schultze's (1992) discussion of *Holodipterus* is also erroneous in a number of respects. Details of the morphology of that genus are set out in Pridmore et al. (1994). For example, the palate has a denticulated surface with denticles on the parasphenoid (Pridmore et al., 1994, figs 8, 47, 49). The denticles are subject to renewal at several periods during the life history of an animal, and individual denticles are covered with intervening 'primitive' dentine during some phases of renewal (Schultze, 1992: 42). This pattern is totally unlike that of *Speonesydrion* (Campbell & Barwick, 1983; 1984), a comparison suggested by Schultze. The marginal ridges are present, and are more obvious on some species, especially at some stages of resorption (Pridmore et al., 1994, figs 4, 29, 73, 96), but in other specimens they are expanded depending on how much resorption has taken place. Contrary to the statement by Schultze (1992: 42), the preorbital cheek has the same cutaway ventral edge as in *Griphognathus*, as was well shown by Campbell & Smith (1987, fig. 8). Schultze (1992) suggested that it is like the sur-

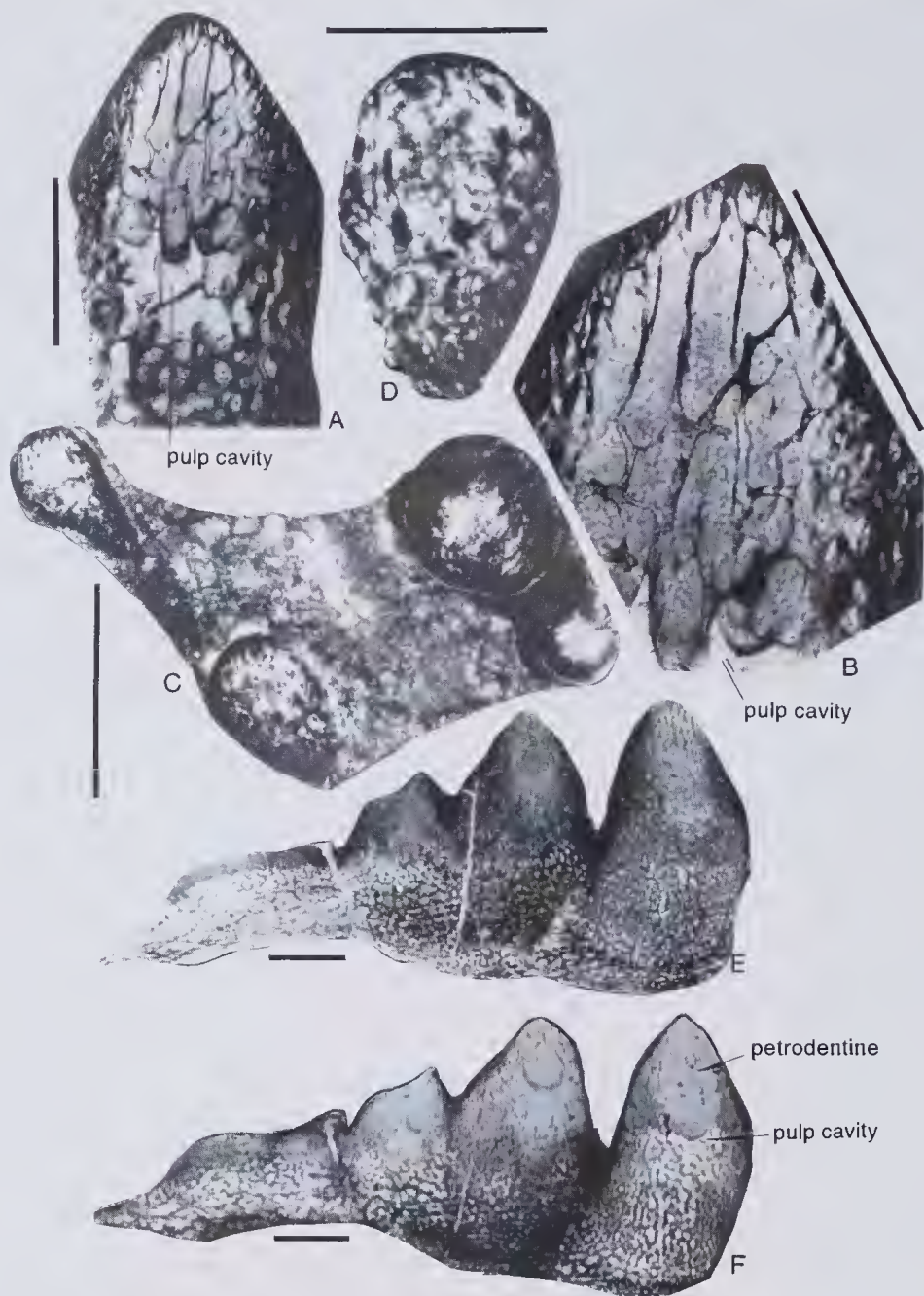


FIG. 32. *Seaumenacia curta* Whiteaves. A-D, optical sections of ANU49092. A, vertical section of the most distal tooth showing the large basal pulp cavity surmounted by dentine, surrounded by dark tissue into which the pulp canals extend. B, enlargement of same, showing the absence of dentine tubules and the cross-textured mass of dentine. C, part section of tooth rows cut from the same specimen; note that close to the tip of the tooth the hard central dentine is present. D, enlargement of the bottom left tooth in C; note the pulp centres within the dentine. E, F, two views of the section figured by Denison (1974, fig. 5). The mounting medium has been recrystallised making the definition worse than in the original figures. E is under single polarised light, and F is crossed polarised light. Note the absence of basal pulp cavity beneath any tooth. Scales A-C = 1mm; D = 0.5mm; E, F = 1mm.

face of *Chirodipterus*, but in fact there are no similarities; it is difficult to see how such a conclusion could be made. In comparing Fig. 33 in this paper with fig. 8 in Campbell & Smith (1987), we note that the ventral edge of the cheek in *Holodipterus* has a considerable gap between the edge of the cheek and the mandible. In addition, the marginal ridges on the palate are nothing like the ridges of *Chirodipterus* or *Speonesydrion* (Campbell & Smith, 1987; Campbell & Barwick, 1984) as suggested by Schultze (1992). Nowhere does Schultze's work comment on the method of making marginal palatal ridges by resorption of the surface on the inner parts of the plate, or of the production of bosses on the palate by failure to resorb parts of denticulated surface during successive episodes. Although when Schultze wrote there was no evidence of basihyal-basibranchial bones in *Holodipterus*, but these are now available Pridmore et al. (1994, figs 29, 32, 57).

In view of Schultze's discussion, we must emphasise that the presence of denticles in the mouth does not indicate a primitive dentition. Denticles are present in a variety of different genera, and we are in no doubt that they have evolved several times to meet different requirements. We chose to use the term 'denticulated' to characterise one group of dipnoans, because that seemed to be an obvious feature of one group. This may have been an unfortunate choice of a term, but it does not permit a misinterpretation of the remainder of the discussion.

Schultze also noted that *Holodipterus* was a food crusher in its feeding, whereas the denticulated group is not so. We point out that *H. (H.) longi* (Pridmore et al., 1994) has a mandible like that of *Griphognathus*, its median area being reduced in length. This mandible also has an adductor pit that is similar to that in other species of *Holodipterus*, and its teeth have been almost completely removed by resorption. In other words this species is different from the basic outline of *H. gogoensis*. The question we now have to ask ourselves is: does the presence of the teeth mean that the group is a tooth-plated form; or does the fact that no true tooth-plates are developed in *Holodipterus*, mean that the teeth were developed secondarily in a genus that was initially a 'denticulated' form? In connection with this argument we point out that in *Holodipterus* the teeth are different in histology from the teeth of other tooth-plated species (Campbell & Smith, 1987), and that they are resorbed periodically from the mesial part of the mouth, the evacuated surfaces becoming occupied with denticles. The latter

view will be rejected by cladists because it is less parsimonious than the former since it requires two developments of teeth within the dipnoans. However, such a parsimonious view is irrelevant, in that it obscures relationships based on biological similarities. We acknowledge that such a 'parsimonious' view will be adopted by some workers, but point out that parsimony applied in such circumstances is unacceptable. In this type of enquiry, parsimony may be used to choose between two hypotheses which have equal merit in explaining a set of observations. It should not be used to generate the hypotheses. In addition, we draw attention to the quote in the paper by Schultze & Marshall (1993): 'And if you get only one tree, but you cannot explain it biologically – start all over again'.

Uranolophus is said by some workers to be different from other denticulated genera in the form of the parasphenoid. Denison in his original paper indicated that it was long and thin, stretching forwards almost to the anterior end of the pterygoids. Campbell & Barwick (1988b) attempted to show that the plate was short, rather like the parasphenoids in such other groups as *Griphognathus*, and that the boundaries of the parasphenoid outlined by Denison were cracks in the palate. Schultze (1992) indicated that the interpretation of Denison was correct, reproducing a drawing in his fig. 1 and photographs in fig. 3 to support this view. Even so, he notes that 'such a parasphenoid is unique within the dipnoans'. We wish once again to dispute his interpretation of the outline on 6 arguments. 1) So far as we are aware, the parasphenoid is a bilaterally symmetrical median bone. Even in those genera in which the dorsal edge of the parasphenoid is expanded, the shape of both dorsal and ventral edges should be symmetrical relative to the midline. This is not so in the inferred outline of Denison. 2) If the shape is as shown by Schultze, 1992, fig. 1B, with the posterior outline skewed, this does not match the position of the dorsal edge as shown by Campbell & Barwick (1988b, fig. 1E). 3) The pituitary is known to have a double origin — part of it is a ventral growth from the braincase, and the other from the pharynx. In *U. wyomingensis* the pituitary fossa (Campbell & Barwick, 1988b, fig. 1E), is situated about one third of the length of the palate from the posterior end, which is its position in other Devonian dipnoans. What is more, the palate is thin, and the hypophysial stalk would have to be situated in approximately the same position. The organisation is very similar to that of *Griphognathus whitei*, in which the parasphe-

noid is of normal Devonian type. 4) We simply controvert the view that other specimens of *U. wyomingensis* in which the palates are incomplete show that the details indicate an elongate parasphenoid. 5) The palate is not thick, but it has thickened edges in certain places as is common in *Griphognathus*. Such thickenings are correlated with its peculiar mode of feeding (Campbell & Barwick, 1988b, fig. 7A). This is the specimen on which Schultze (1992, fig. 1B) is based, and in which the anterior end of the parasphenoid follows the outline of the depression. 6. Comparison with outgroup species such as *Diabolepis* does nothing to add to the argument. What such argument shows is that attention to comparative studies with genera of doubtful affinity causes observers to view what they think are appropriate structures, rather than what is to be seen. It biases basic morphological work towards bad observation. In summary we see no reason apart from cracks on the palate to assume that the parasphenoid is long and narrow as suggested by Denison (1968) and Schultze (1992).

We were mistaken in stating that the 'denticulated' group had no adsymphysial plate in the lower jaw of *Griphognathus* (Campbell & Barwick, 1984, p. 163). Such a plate is not clear in *G. whitei*, but it is present in *Griphognathus sculpta*. This item will have to be removed from the features used to outline the 'denticulated' group (Campbell & Barwick, 1990).

The group of *Griphognathus*, *Rhynchodipterus*, *Soederberghia* and *Fleurantia* is not monophyletic; Schultze (1992) recognised this. *lowadipterus* cannot be related to *Holodipterus* as a long-headed form in which the the mandible is short. Compare the mandible of *H. (H.) longi* (Pridmore et al., 1994, fig. 33) with that of other specimens of *Holodipterus* figured elsewhere in the same paper. *Holodipterus* is a member of the so-called 'denticulated' group, which has become shorter headed than other members of that group as a result of the development of marginal teeth which are progressively resorbed. It is not possible from available material of *lowadipterus* to indicate what its relationships are. Further evidence of the structure of its palate is necessary.

Schultze (1992) was of the opinion that the longer posterior part of the skull permitted a larger mass of adductor mandibulae musculature to fit under the skull roof; this is certainly correct for *lowadipterus* which is also characterised by a very forward position of the eye. Comparison of Schultze's (1992) figures of *lowadipterus* and *Holodipterus* (Fig. 3) show that the forward posi-

tion of the eye relative to the median bones of the skull roof B and C, is not the only factor involved in providing a larger space for muscles, because the operculars of the two genera lie in a completely different position relative to the Y bones. In dipnoans, the anterior edge of the opercular is situated against the quadrate, which defines the front wall of the gill chamber. We conclude, therefore, that in *lowadipterus* the gill chamber was situated further back relative to the Y bones than in *Holodipterus*. This is important because it suggests that the elongation of the posterior part of the head and the cheek is the result not only of the forward position of the eye, but also the position of the gill chamber. Consequently the functional significance of the position of the gill chamber has to be investigated as well as the space for adductor muscles. It seems probable that elongation of the head may be the result of more than one factor. In addition to muscle space and gill chamber position, we consider that elongation of the parasphenoid to roof over the buccal chamber, in which air was held prior to its being forced down into the lungs, could also be significant (Campbell & Barwick, 1988a). Information on the position and size of the parasphenoid in *lowadipterus* is not at present available, and so we cannot make a judgement about how it fits above the gill chamber.

In summary, we see no evidence that the extension of the posterior part of the head and the elongation of the cheeks, is likely to outline a distinctive group of dipnoans.

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CONSUMPTION OF *IDIOSPERMUM AUSTRALIENSE* SEEDS BY THE MUSKY RAT KANGAROO, *HYPSPRYMNODON MOSCHATUS* (Marsupialia: Potoroidae). *Memoirs of the Queensland Museum* 42(2): 438, 1998:—Information on the feeding ecology of *Hypsiprymnodon moschatus* Ramsay, 1876, a primitive diurnal marsupial, is scant. Our present knowledge has mainly come through the PhD research of Andrew Dennis (unpubl., James Cook University), carried out on the Atherton Tablelands, NE Queensland.

The current study is based on our daylight observations of Musky Rat Kangaroos (April 16 to May 4, 1997) in the Cooper Ck catchment, Cape Tribulation NP. During this period, Musky Rat Kangaroos were twice observed eating the seeds of *Idiospermum australiense*. Consumption of these seeds causes cattle deaths (Everist, 1981). *Idiospermum australiense* is relatively common in the study site, about 10m from Cooper Ck in an area of lowland complex mesophyll vine forest, and often grows in small stands of 5–10 plants. The ground beneath these plants is littered with seeds of all ages; 100 seeds were counted in the particular stand studied. Other stands occur throughout the surrounding rainforest. The fruit ranges from 80–100mm in diameter. It has a brown pericarp which splits to reveal a seed with 3–6 large cotyledons. April is a month of low fruit abundance in this area; fruiting species include candlenut (*Aleurites moluccana* or *A. excelsa*) and the fig (*Ficus variegata*). During 106 hrs of observation, we recorded 44 instances of feeding at the site. On April 18 at 2:25pm, a Musky Rat Kangaroo was seen to pick up an *Idiospermum* seed with its forelimbs, then chew it for about 30 seconds, before dropping it and hopping away. This was repeated at 3:35pm. The same seed was chewed on both occasions. It appeared to be a fairly old seed with no pericarp. Approximately one fifth of the seed had been removed and characteristic teeth marks were evident.

Idiospermum seeds at several stands were examined to determine the percentage that had been chewed. To establish the age of seeds, we recorded whether or not the pericarp was intact and whether it was fresh or brown (the dark colour is indicative of older seeds). The state of the seed; untouched, chewed, or scratched was also recorded. Freshly chewed seeds are almost white; they darken as they oxidise over a few days (presumably by polyphenol-oxidase activity). We examined 375 seeds and found that 51% were chewed, 40% were untouched, and 9% were scratched. Seeds with only their pericarps chewed were not observed during this study. In most cases the seed had been chewed where the pericarp was

already broken. Most chewed seeds had only a small percentage of the cotyledons removed, and these seeds were of all ages. Older seeds were more heavily chewed. The chew marks were similar to those made by the Musky Rat Kangaroo that we had previously observed.

We seeded the stand of *Idiospermum* with 20 *Aleurites moluccana* seeds to see whether *H. moschatus* showed a preference for either of the two species. *A. moluccana* seeds were picked from a fallen branch using gloves to avoid biasing the animal's choice by touching them with bare hands. The seeds were set out at 7:00am and collected at 5:00pm for 5 days. The first day, 10 of the 20 seeds were chewed or removed. None were touched during the following 4 days. The presence of the *A. moluccana* seeds did not seem to deter *H. moschatus* from feeding on the *Idiospermum* seeds. On the third day of seeding, 10% of the *Idiospermum* seeds were freshly chewed (7/70). On the fifth day, 4% (3/72) were freshly chewed. The total percentage chewed rose from 48% before we seeded to 57% on the fifth day. It seems reasonable to suggest that *H. moschatus* were not feeding on *A. moluccana* seeds in preference to *Idiospermum* seeds.

We also observed *H. moschatus* eating and dispersing the large seeds of the cycad *Lepidozamia hopeii*, another species assumed toxic to most mammals (Everist, 1981). A Musky Rat Kangaroo was observed (May 4) picking up, chewing, and then running off with a *L. hopeii* seed. This occurred 3 times in a 3-hour period. Several of the seeds left on the ground were also chewed. Behaviour similar to this observation had been observed by the landowners on previous occasions (P. Hewitt, pers. comm).

Acknowledgements

For their hospitality, we thank Prue and Neil Hewitt (owners of the Cooper Ck property on which the observations were made). Allison Drew (a School for International Training student) was supported in part through the Australian Tropical Research Foundation and the Cape Tribulation Tropical Research Station.

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ABERRANT PLUMAGES IN BIRDS OF PARADISE (PARADISAEIDAE)

CLIFFORD B. FRITH AND DAWN W. FRITH

Frith, C.B. & Frith, D.W. 1998 06 29: Aberrant plumages in birds of paradise (Paradisaeidae). *Memoirs of the Queensland Museum* 42(2): 439- 443. Brisbane. ISSN 0079-8835.

More than 6,000 bird of paradise (Paradisaeidae) skins were examined in museum collections. Aberrant plumage was recorded in 12 of the 42 species, and less than 1% of the total sample. Most aberrant individuals exhibited partial albinism in showing a few white feathers, or a patch of them, in otherwise normal plumage. Two specimens were predominantly white. Two specimens of *Cnemophilus macgregorii*, two of *Ptiloris magnificus*, and one of *Cicinnurus respublica* showed other aberrant plumage. All aberrancies are described and discussed, and several of these are illustrated. □ *Paradisaeidae, aberrant plumage, partial albinism.*

Clifford B. Frith and Dawn W. Frith, Honorary Research Fellows of the Queensland Museum, 'Prionodura', P.O. Box 581, Malanda, Queensland 4885, Australia; 10 December 1997.

During recent visits to the majority of world museums (see acknowledgements, and Frith & Frith, 1997b) holding significant numbers of birds of paradise, we examined all specimens of the Paradisaeidae. One of us (CBF), measured 5,677 of the sexed skins. Studies resulting from this work to date include the description of some previously unknown plumages (Frith, 1987, 1996; Frith & Harrison, 1989), reassessment of some taxa (Frith & Frith, 1996a,b, 1997b), a review and summary of biometrics (Frith & Frith, 1997a; Frith, 1997) and a review of a classification of the phylogeny and systematics of the family (Frith & Beehler, in press). In addition to these more quantitative studies, note was made of specimens exhibiting aberrant plumage of any kind. The most commonly found type of aberrant plumage was partial albinism; which may involve some, to most, of the otherwise normally-pigmented plumage of a bird being white (whole or part feathers may be white).

This paper describes and discusses bird of paradise specimens showing visually noticeable aberrant plumage characters. Where registration or catalogue numbers include a prefix on the specimen label these are included but in remaining cases only the number appears. In the following, capitalised and/or numbered colours are those of Smithe (1975) while uncapitalised ones are those we consider more helpful than other options. The sequence of genera and species and names used below are those presented in a forthcoming review of the systematics of the family (in Frith & Beehler, in press).

CRESTED BIRD OF PARADISE *Cnemophilus macgregorii* DeVis, 1890. ♀ and immature ♂

plumages of this species and of congeneric Loria's Bird of Paradise *C. loriae* were known to be generally olive-green until a distinctive grey juvenile plumage was found in both species (Frith, 1987; Frith & Harrison, 1989). Two specimens of *C. macgregorii* were subsequently found to be in a previously unrecorded, aberrant 'fawn' plumage (see Frith, 1996). As the fawn plumage in this taxon has not been illustrated, an unsexed specimen CG1898 1381 from the Astrolabe Mts, Papua New Guinea (Muséum National d'Histoire Naturelle, Paris) is shown here (Plate 1A). The pale bill (normally black or blackish) of this specimen strongly supports the conclusion that the plumage is aberrant and not merely faded or foxed. It is best described as non-eumelanic schizochroism (Harrison, 1985). Two of 183 specimens examined (1.1%) had aberrant plumage.

MACGREGOR'S BIRD OF PARADISE *Macgregoria pulchra* DeVis, 1897. Specimen 1305 in the Staatliches Museum für Naturkunde, Stuttgart shows partial albinism in having a few white feathers in its abdomen plumage. It is labelled as ♂ but is quite possibly a ♀ in view of its small size (see Frith & Frith, 1997b). One of 76 specimens examined (1.3%) had aberrant plumage.

PARADISE CROW *Lycorax pyrrhopterus* (Bonaparte, 1851). Specimen 60787, an adult ♀ in the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt is a partial albino. It displays typical plumage except for a single pure white feather in its mantle. Specimen 6921, an adult ♀ in the Museum Zoologicum Bogoriense, Bogor is a partial albino. It has a large patch of

**A****B****C****D****E****F**

white feathers in its central abdomen plumage. Two of 224 specimens examined (0.9%) had aberrant plumage.

CURL-CRESTED MANUCODE *Manucodia comrii* Sclater, 1876. Specimen 784692, an adult ♀ in the American Museum of Natural History, New York has several white feathers in its throat, chest and abdomen plumage. One of 79 specimens examined (1.3%) had aberrant plumage.

SPLENDID ASTRAPIA *Astrapia splendissima* Rothschild, 1895. Specimen 342102, a ♀ in the American Museum of Natural History shows partial albinism. Its head, nape, throat and upper chest are white with a few black flecks. The upperwing (i.e., greater coverts) is white as are the inner primaries and secondaries plus a tertial on one side. There are a few odd white feathers in the breast, abdomen and vent. The legs and feet are conspicuously piebald with all of the claws pale.

Specimen 302958, an undoubted ♀ (its oocytes being drawn on the label) in the American Museum of Natural History has a single iridescent magenta (2) adult ♂-like feather in upper breast - also several larger lower back feathers have half the vane white. Two of 204 specimens examined (1%) had aberrant plumage.

STEPHANIE'S ASTRAPIA *Astrapia stephaniae* (Finsch & Meyer, 1885). Specimen 1900.2.19.16, an adult ♂ in the Natural History Museum, Tring is a partial albino in showing several white feathers in the lower green throat and crown plumage, plus one white feather in the nape. Specimen 12.478, an adult ♂ in the Zoologische Staatssammlung, München is in normal plumage, save a single white feather in its crown. Two of 291 specimens examined (0.7%) had aberrant plumage.

MAGNIFICENT RIFLEBIRD *Ptiloris magnificus* (Vieillot, 1819). An unnumbered adult ♂ in the Rijksmuseum van Natuurlijke Historie, Leiden is aberrant. It lacks almost all colour, there being a mere trace of iridescent purple-blue between its fore-eyes and nostrils only. This bird is

a washed-out matte, pale-smoky, brownish-grey above (somewhat reminiscent of *Semioptera*). The wings and tail are paler (see Plate 1B). There is a single teardrop-sized, and shaped, spot of typically normal iridescence on one central tail feather (12mm above its tip). The crown feathering is typically scale-like, but is matte, smoky, brownish-grey and is soft in texture. The breast shield is normal in shape and structural stiffness. It is slightly glossy, brownish-grey with no iridescence. The tract of feathers between the sides of the breast shield and mantle are near velvet black, being dark brownish-grey. Remaining under parts are blackish-brown (closest to 121), with no sign of the usual claret red or green sheens. Quill shafts of primaries, secondaries and rectrices are white, clearly emphasizing this abnormal plumage. A Dutch publication noted the bird had certainly not been preserved in fluid (Büttikofer, 1895) and in any event, iridescence becomes evident in fluid-preserved specimens when dried out (M. LeCroy, in litt.). This specimen is most appropriately described as demonstrating dilution or leucism (C.J.O. Harrison, in litt.).

Specimen CG1930 No. 440, an adult ♂ in the Muséum National d'Histoire Naturelle, Paris has the rear chin and throat feathers of its otherwise typically iridescent breast shield glossy-blackish each with a pale, off-whitish or very pale buff, centre and broad outer edging (see Plate 1C). Two of 524 specimens examined (0.4%) had aberrant plumage.

PALE-BILLED SICKLEBILL *Drepanornis bruijnii* Oustalet, 1880. Specimen 10239, an immature ♂ in the Staatliches Museum für Naturkunde, Stuttgart shows partial albinism. The terminal two thirds of the second outermost primary of its right wing are pure white save that its central shaft is darkly pigmented. One of 151 specimens examined (0.7%) had aberrant plumage.

MAGNIFICENT BIRD OF PARADISE *Cicinnurus (Diphyllodes) magnificus* (Pennant, 1781). Specimen CII289, III, 174, an adult ♂ in the Staatliches Museum für Tierkunde, Dresden is a

FIG. 1. A, unsexed and mounted *Cnemophilus macgregorii* Muséum National d'Histoire Naturelle specimen CG1898 1381. B, adult ♂ *Ptiloris magnificus* Rijksmuseum van Natuurlijke Historie unnumbered specimen. C, throat and breast detail of adult ♂ *P. magnificus* Muséum National d'Histoire Naturelle CG1930 No. 440. D, dorsal view of adult ♂ Staatliches Museum für Tierkunde C17848 *Paradisaea minor* (left) SMTC11289, III, 174 *Cicinnurus (Diphyllodes) magnificus* (right). E, dorsal view, and F, ventral view, of (left) adult ♂ Staatliches Museum für Naturkunde SNHM15522 *Cicinnurus (Diphyllodes) respublica* and (right) a typically normally-plumaged adult ♂ (SNHM 44502) of that species in the same collection.

partial albino. It is white throughout except that its underparts (chin and throat excluded) are normal iridescent green and it has a few brownish back and wing feathers and one or two mustard yellow tertials (Plate 1D).

Specimen 454366, an adult ♂ in the American Museum of Natural History is also a partial albino. It has several white feathers in its upperparts, and a few in the underparts. The primaries and secondaries and most of crown, nape and cape is white. Its tarsii and claws are whitish and the toes are piebald. Part of this specimen is illustrated by a colour photograph in Purcell & Gould (1988: 75, pl. 52).

Specimen 454367, an adult ♂ trade skin lacking the central rectrices (from unknown locality) in the American Museum of Natural History, is almost entirely white. It has one almost normally pigmented secondary with scattered blackish feathers (tipped in green) in its ventral plumage, more so in the flanks. Specimen 678406 in the American Museum of Natural History, a flat, legless and distorted adult ♂ trade skin (lacking the central rectrices), has plumage similar to that of 454366, above. Four of 600 specimens examined (0.7%) had aberrant plumage.

WILSON'S BIRD OF PARADISE *Cicinnurus (Diphyllodes) respublica* (Bonaparte, 1850). Specimen SNHM 15522, an adult ♂ in the Staatliches Museum für Naturkunde, Stuttgart is unique in that all its underparts, and most of the upperparts, are a deep rich fawn colour (27). However, the normal yellow cape and the red of the central back (bordered posteriorly by a black line) and wing patch are present. The back and secondary coverts are, however, less red and more orange than usual. The bare head skin is not black (as in all other dry skin specimens) but dark brown, suggesting it may not have been the usual blue colour in life. The usually dense and plush black head and throat feathers are silvery-buff in this bird. The central tail 'wires' are missing, presumably moulted. This individual's appearance fits that of non-eumelanic schizochroism (Harrison, 1985) (see Plate 1E & F). One of 94 specimens examined (1.1%) had aberrant plumage.

LESSER BIRD OF PARADISE *Paradisaea minor* Shaw, 1809. Specimen SMT C 17848, an adult ♂ in the Staatliches Museum für Tierkunde, Dresden is extensively a partial albino. It is entirely glossy white save for a pale yellow wash on the crown. It is even paler, on mantle and wing-cov-

erts. It has a single pale brown tertial, wing and tail feather (Plate 1D). One of 565 specimens examined (0.2%) had aberrant plumage.

BLUE BIRD OF PARADISE *Paradisaea (Paradisornis) rudolphi* (Finsch, 1885). Two colour photographs of a live partial albino ♀ *P. rudolphi*, taken under controlled conditions in New Guinea, appear in Gilliard (1953: 441). This bird is in typical plumage but shows a white patch of tertials, a few white primaries, secondaries and lesser upper wing coverts, and a white terminal third to its outer left tail feather. None of the 90 museum specimens examined showed schizochroic characters or those of any other aberrant plumage.

DISCUSSION

Birds of paradise showing even the smallest amount of aberrant plumage are few and represent less than 1% of the above species samples combined. In examining more than 6,000 museum skin specimens (including unsexed individuals) and in reviewing the literature only the above individuals came to our notice. Clearly, most of these examples of aberrant plumage involve individuals showing partial albinism. In most cases there are no more than a few white feathers, or a patch of them, in otherwise typically normal plumage. Given the large sample size, partial albinism is clearly rare, while a true albino (entirely white plumage throughout with associated pale iris) individual remains unrecorded, in the Paradisaeidae. This said, it is possible that such unusual looking individuals were specifically sought or purchased by field collectors and traders because of their greater value as novelties.

The single adult-♂ like feather in an otherwise normally-plumaged ♀ *A. splendidissima* is possibly an example of the well-known phenomenon of an older ♀ individual bird showing some sign of adult ♂ nuptial plumage.

Of the above documented abnormal bird of paradise plumages, those of *Cnemophilus macgregorii*, *Ptiloris magnificus* and *Cicinnurus respublica* are the most noteworthy. The aberrant plumage of the *P. magnificus* specimen is apparently the result of a reduction in the black pigment eumelanin which results in the bird having a distinctly washed-out or 'faded' appearance but with no tendency toward a 'warming' of appearance by fawn colouration. The above aberrant plumages of both *C. macgregorii* and *C. respublica* are noteworthy, however, as their clearly 'fawn' and 'warm' colouration is generally simi-

lar to the perfectly normal but 'faded' plumage appearance of the Standardwing Bird of Paradise *Semioptera wallacii*. It has been suggested that this odd but perfectly typical plumage morphology of *S. wallacii* may be due to its island isolation in the absence of other polygynous birds of paradise (Graves, 1995). This scenario could also be true of *C. respublica* which shows the most similarly 'fawn' aberration (although it does share its island ranges with the Red Bird of Paradise *Paradisaea rubra*). The authors would be interested to learn of any additional examples of aberrant plumages in the Paradisaeidae.

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A MATURE CUPULE OF *LEPTOSTROBUS* (CZEKANOWSKIALES) FROM THE LATE TRIASSIC OF QUEENSLAND

H.T. CLIFFORD AND N. CAMILLERI

Clifford, H.T. & Camilleri, N. 1998 06 29: A mature cupule of *Leptostrobus* (Czekanowskiales) from the Late Triassic of Queensland. *Memoirs of the Queensland Museum* 42(2): 445-447. Brisbane. ISSN 0079-8835.

A single bivalvate cupule of *Leptostrobus* is reported from Upper Triassic sediments of the Ipswich Coal Measures. This record is the oldest known for the genus. □ *Leptostrobus*, Triassic, Australia.

H. Trevor Clifford and Natalie Camilleri, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 21 February 1998.

The Czekanowskiales were first recognised as occurring in Australia when Jones & de Jersey (1947) recorded *Czekanowskia tenuifolia* (Johnston) from Late Triassic Ipswich Coal Measures. The species had originally been described by Johnston (1887) from Lord's Hill near Hobart. At that date they were regarded as belonging to *Baiera* a genus of Ginkgoales. On the basis of its epidermal structure the species *B. tenuifolia* was transferred to *Czekanowskia* by Jones & de Jersey (1947).

The similarity of *B. tenuifolia*, as it was then known, to *Czekanowskia microphylla* had been noted by Walkom (1925), indicating an overlap in gross morphology of the two species.

In addition to *Czekanowskia* Jones & de Jersey (1947) also recorded a single presumed cupule-bearing axis of *Leptostrobus* in the same deposit. The cup-shaped organs are much smaller than the cupule described here and so may be regarded as immature.

Although *Czekanowskia* and *Leptostrobus* have not been encountered in organic connection, their frequent joint occurrence is taken to indicate that they represent the foliage and cupules of the same taxon.

STRATIGRAPHY

The specimen described was exposed by the splitting of fossiliferous, siltstone float close to a dirt track beginning at the end of Thomas St, on the W side of 'Castle Hill', Blackstone. On the basis of lithology the specimen is considered as being in situ.

Whether these siltstones represent a horizon within the Rhaetian Aberdare Conglomerate or the Carnian Blackstone Formation is difficult to determine with certainty, because the two are separated by an unconformity, and siltstones within the Aberdare Conglomerate are lithologi-

cally similar to some beds in the Blackstone Formation (Cranfield et al., 1976). Nonetheless, it is certain the siltstone float is Upper Triassic (de Jersey, 1975).

SYSTEMATIC PALAEOBOTANY

Division Gymnospermae
Order Czekanowskiales Harris & Miller
***Leptostrobus* Heer**
***Leptostrobus cookii* sp. nov.**
(Figs 1-2)

ETYMOLOGY. For Alex Cook in recognition of his enthusiasm for all things geological.

MATERIAL. Holotype: QMF37262a, (convex) Ipswich, Queensland 27°37'39"S, 152°47'58"E; QMF37262b, (concave) counterpart.

DIAGNOSIS. Coalified cupule consisting of two similar oppositely placed valves obovate in outline. Internal surface with slightly raised longitudinal ribs. Seeds and ovules missing.

DESCRIPTION. The cupule is completely coalified and no cell detail is available. The scales are obovate in outline, 16mm long and 12mm broad. The thickening of the valve can be estimated from the fractured surfaces. Towards its apex the valve is about half as thick as at its base (2.5-3.0mm).

The inner surface of one scale is concave and that of the other is convex which suggests that the latter has been pushed into the former during the process of fossilization (Figs 1, 2).

DISCUSSION

Well-developed cupules of *Leptostrobus* have not been reported previously from Australia although its associated foliage *Czekanowskia* (as *Baiera*) has been known for more than a century. Since the Ipswich area, in particular, has been intensively collected over a long period it is clear the cupules are rare.



FIG. 1. Internal surfaces of the valves of a mature cupule of the holotype of *Czekanowskia cookii* sp. nov. A, QMF37262a; B, QMF37262b (surface convex due to compression).

As judged by the rotting vegetation on the floor of a small lake at J.C. Slaughter Falls in the Mt Coot-tha Reserve near Brisbane this situation is perhaps to be expected. Although leaves of *Eucalyptus* and *Corymbia* are abundant on the lake-

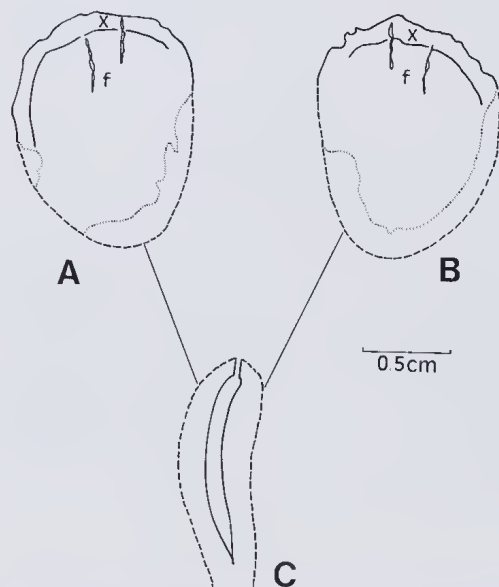


FIG. 2. Diagrammatic representation of a mature cupule of the holotype of *C. cookii* sp. nov. based on the valves illustrated in Fig 1. A, valve QMF37262a. B, valve QMF37262b. C, hypothetical reconstruction of cupule. x = valve margin, f = cracks in wall of valve.

bed the woody fruits of the two genera are rare (Clifford, 1990).

Seed-bearing structures of any kind are likewise rare in the Ipswich beds which were also laid down in freshwater. Aside from *Leptostrobus*, the only other seed-bearing structures recorded in the sediments are *Fraxinopsis major* and a possible crustosperm megasporophyll (Hill et al., 1966; Jones & de Jersey, 1947).

In his original description of *Czekanowskia tenuifolia* Johnston (1887) referred to abundant associated reproductive structures in the material. He provided detailed descriptions and some figures but

these are difficult to interpret and so will not be considered further.

The presence of *Czekanowskia* in the Triassic of Australia has been long over-looked. In the paper in which the Order was established (Harris & Miller, 1974) no reference was made to the work of Jones & de Jersey (1947) which was also apparently unknown to either Taylor & Taylor (1993) or Sporne (1974) who claim the *Czekanowskia* extended only from the Jurassic to the Cretaceous.

According to Max Banks (pers. comm.) the foliage reported from the New Town shales at Lord's Hill are Ladinian and so are slightly older than the Ipswich deposits which were laid down about 235MA (Harland et al., 1989). The geological range of the *Czekanowskia* therefore is to be extended back from the early Jurassic to the Middle Triassic.

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FIRST RECORD OF CAYTONIA IN AUSTRALIA. *Memoirs of the Queensland Museum* 42(2): 448. 1998:- An axis bearing two rows of shortly stalked ovule-bearing cupules and attributable to *Caytonia* has been observed in Lower Jurassic sandstones belonging to the Marburg Formation, at Durikai in SE Queensland. Support for the identification is provided by impressions of *Sagenopteris rhoifolia* in the same beds (Hill et al., 1966). Though not as yet found in organic connection *Caytonia* and *Sagenopteris* regularly co-occur and are usually regarded as being the seed-bearing organ and foliage of the same taxon (Taylor & Taylor, 1993).

Division PTERIDOSPERMAPHYTA
Order CAYTONIALES H.H. Thomas
Family CAYTONIACEAE Pilger & Melchior
Caytonia tierneyi sp. nov.

Etymology. For Paul Tierney the collector.

Material. Holotype: QMF39005, Durikai 38°12'S, 151°37'E.
Paratype: QMF35881, same locality.

Diagnosis. An unbranched axis bearing two rows of alternating co-planar, shortly stalked, transversely elliptical cupules each bearing several ovules.

Description. Axis at least 11.5mm long bearing two rows of cupules each about 1.0-1.2mm x 2.0mm, borne on stalks up to 1mm long. Both axis and cupule stalks have a median groove on their abaxial surfaces. (Figs 1, 2).

Remarks. The new species differs from others of *Caytonia* in that the cupules are elliptical rather than spherical and are arranged alternately instead of oppositely or suboppositely on their axis (Thomas, 1925).



FIG. 1. Inflorescence of *Caytonia tierneyi* sp. nov. with one cupule containing ovules. Holotype QMF39005. Scale bar 1mm.



FIG. 2. Mould of an inflorescence of *Caytonia tierneyi* sp. nov., Paratype QMF35881. Scale bar in mm.

Acknowledgements

Natalie Camilleri and Alex Cook are thanked for the photographs.

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H. Trevor Clifford, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 10 March, 1998.

FRASNIAN GASTROPODS FROM THE BONAPARTE GULF BASIN, WESTERN AUSTRALIA

ALEX G. COOK

Cook, A.G. 1998 06 29: Frasnian gastropods from the Bonaparte Gulf Basin, Western Australia. *Memoirs of the Queensland Museum*. 42(2): 449-457. Brisbane. ISSN 0079-8835.

Eight taxa of gastropods are described from the Late Devonian (Frasnian) Westwood Member of the Hargreaves Formation, Bonaparte Gulf Basin, Western Australia. Of these *Ningbingia robertsi* gen. et sp. nov., *Aglaoglypta veeversi* sp. nov., *Pseudomphalotrochus bonapartensis* sp. nov., *Westwooditrochus weestwoodensis* gen. et sp. nov., and *Plagiothrya curlyjigga* sp. nov. are new. The remaining taxa are left in open nomenclature. *Pseudomphalotrochus*, *Aglaoglypta* and *Plagiothrya* relate strongly to European and/or North American Devonian taxa. □ *Devonian, Frasnian, gastropods, Western Australia.*

Alex G. Cook, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 6 August 1997.

The Westwood Member of the Hargreaves Formation is an abundantly fossiliferous unit which crops out near Westwood Ck, in the vicinity of Cape Dommet, Bonaparte Gulf Basin, WA. The member contains a diverse assemblage of algae, corals, stromatoporoids, brachiopods, conodonts, fish plates, bivalves and gastropods, of which, only the brachiopods (Roberts, 1971) and conodonts (Druce, 1969) have received taxonomic attention.

The most recent stratigraphic and sedimentologic summaries of the Hargreaves Formation are given by Mory & Beere (1988) and Mory (1990) who both indicated reefal and back-reefal depositional environments for this unit. The age of the Westwood Member was given as Frasnian by Druce (1969) and Roberts (1971) and subsequent studies (Mory & Beere, 1988; Mory, 1990) have confirmed this age. This paper describes the modest gastropod faunule from the Westwood Member. All gastropods described in this work come from outcrops on, or adjacent to, tidal flats near Westwood Ck. These are:

QML1035 – Westwood Ck, Cape Dommett, tidal flats, 14°51.7' S, 128°30.1' E. Medusa Banks 1:250000 Geological Sheet SD 52-10. Collected Jell & Cook, 1996.

QML1037 – 400m to NE of QML1035, amongst pinnacles of reefal limestone and oncolitic beds. Collected Jell & Cook, 1996.

Phylum MOLLUSCA
Class GASTROPODA

Order ARCHAEOGASTROPODA Theile, 1925
Suborder BELLEROPHONTINA Ulrich & Scofield, 1897

Superfamily BELLEROPHONTOIDEA
M'Coy, 1851

Family BELLEROPHONTIDAE M'Coy, 1851
Subfamily TROPIDODISCINAE Knight, 1956

Ningbingia gen. nov.

ETYMOLOGY. For 'Ningbing' Station, upon which the material was collected.

TYPE SPECIES. *Ningbingia robertsi* sp. nov.

DIAGNOSIS. Large members of subfamily, with narrow, rapidly expanding shell, with wide umbilicus, and an ornament consisting of strongly arcuate ribs.

REMARKS. The narrow crested selenizone, the arcuate ribbing and the shell form identifies the material as belonging to the Tropidodiscinae. It is most similar to *Tropidodiscus*, but is distinguished by its large size and the more arcuate ornament on the whorl face, particularly near the umbilicus. The type species of *Tropidodiscus*, *Bellerophon curvilineatus* Conrad, from the Onondaga Limestone of New York is a moderately large member of the genus (and subfamily). The genotype has a diameter of approximately 28mm (Knight, 1941), contrasting strongly with the tiny species known from Early and Middle Devonian faunas in eastern Australia. For example *T. centrifugalis* (Chapman) of Tassell (1982) from the *Receptaculites* Limestone (Emsian) of New South Wales is close to one third of this size. A small tropidodiscine from the Burdekin Formation (Givetian) of Queensland is only 2.5mm in diameter (Cook, 1997). *Ningbingia* is up to 52mm in diameter, and is proportionately thicker than the genotype, it also possesses strong, arcuate

TABLE 1. Shell measurements for *Ningbingia robertsi* gen. et sp. nov.

Specimen	Diameter (mm)	Width (mm)
QMF35010	18.1	9.5
QMF35059	38.5	17.6
QMF35061	26.5	14.5
QMF35072	52.1	25.5
QMF35118	32.0	18.5
QMF35121	26.0	10.5

ornament in contrast to the fine growth lines of *Tropidodiscus curvilineatus* (Conrad).

***Ningbingia robertsi* sp. nov.**
(Fig. 1A-E)

ETYMOLOGY. For Professor John Roberts.

MATERIAL. Holotype: QMF35059. Paratypes: QMF35054-35058, 35060-35066, 35069, 35071-35074, 35088-35090, 35116-35118, 35121, 35010 all from QML1035.

DIAGNOSIS. As for genus.

DESCRIPTION. Shell medium sized to large, sharply narrow, involute, rapidly expanding shell, up to 38.5mm in diameter and 25.5mm wide (Table 1). Umbilicus up to 1/3 of shell diameter. Selenizone on a crest, narrow, flanked by two weak cords. Ornament consists of strong arcuate ribs curving strongly into the umbilicus, and on the last whorl becomes more arcuate towards the aperture.

Family BELLEROPHONTIDAE M'Coy, 1851

***Aglaoglypta* Knight, 1942**

REMARKS. *Aglaoglypta* Knight 1942 was erected upon *Bellerophon koeneni* Clarke, from the Late Devonian (Frasnian) "Naples" Fauna of New York. Knight (1942) did not provide a list of species included in his concept of the genus, and subsequently little attention has been paid to the taxon. Despite the suggestion (Knight, 1942) and the assertion (Knight et al., 1960) that *Aglaoglypta* represents a subgenus, it is retained here at generic status due to the highly diagnostic pustulate ornament. Species here placed in *Aglaoglypta* are, apart from the type; *Bellerophon tuberculatus* Ferrusac & d'Orbigny of d'Archaic & de Verneuil (1842), *B. maera* Hall, from the Chemung of New York and *B. neleus* Hall & Whitfield (1877) from the Devonian of Nevada. Clarke (1903) listed *B. striatus* Ferrusac & d'Orbigny, *B. tuberculatus* d'Orbigny (a differing authorship attributed than by d'Archaic & de Verneuil) and *B. alutaceus* d'Orbigny as those Devonian *Bel-*

TABLE 2. Shell measurements for *Aglaoglypta veeversi* sp. nov.

Specimen	Diameter (mm)	Width (mm)
QMF35539	13.5	14.0
QMF35016	14.5	17.6
QMF35540	14.5	15.5
QMF35540	13.4	12.7
QMF35568	15.0	14.3

lerophon species with pustulose ornament. I have been unable to access original descriptions of *B. alutaceus*, *B. striatus*, or *B. tuberculatus*, so my assessment of the genus is incomplete. The genus requires a review, by an author with access to the early 19th century literature and the European material.

***Aglaoglypta veeversi* sp. nov.**
(Fig. 1F-J)

ETYMOLOGY. For Professor J.J. Veevers.

MATERIAL. Holotype: QMF35539. Paratypes: QMF35016, 35540-35560 all from QML1035.

DIAGNOSIS. Ornament subdued, pustulate, arranged along fine growth lines.

DESCRIPTION. Small, spheroidal, involute shell, with very narrow umbilicus. Up to 17.5mm diameter, 15.5mm in width (Table 2). Ornament of fine growth lines with papillae arranged in rows upon them. Weak, low crest bearing selenizone. Aperture moderately flared where preserved.

REMARKS. The species differs from the type in having weaker pustules which occupy less space on the whorl surface. *Aglaoglypta tuberculatus* (Ferrusac & d'Orbigny) of d'Archaic & de Verneuil from the Devonian (Eifel) of Paffrath has similar arrangement and strength of the pustules (based on the figure and limited description). *A. maera* (Hall) also has stronger ornament, and a slightly more recurved lip than the Bonaparte species.

Suborder MACLURITINA Cox & Knight, 1960
Superfamily EUOMPHALOIDEA
de Koninck, 1881

Family EUOMPHALIDAE de Koninck, 1881

***Pseudomphalotrochus* Blodgett, 1992**
***Pseudomphalotrochus bonapartensis* sp. nov.**
(Fig. 2)

ETYMOLOGY. From the Bonaparte Gulf Basin.

MATERIAL. Holotype: QMF35087. Paratypes: QMF35067, 35068, 35070, 35075, 35076, 35079-

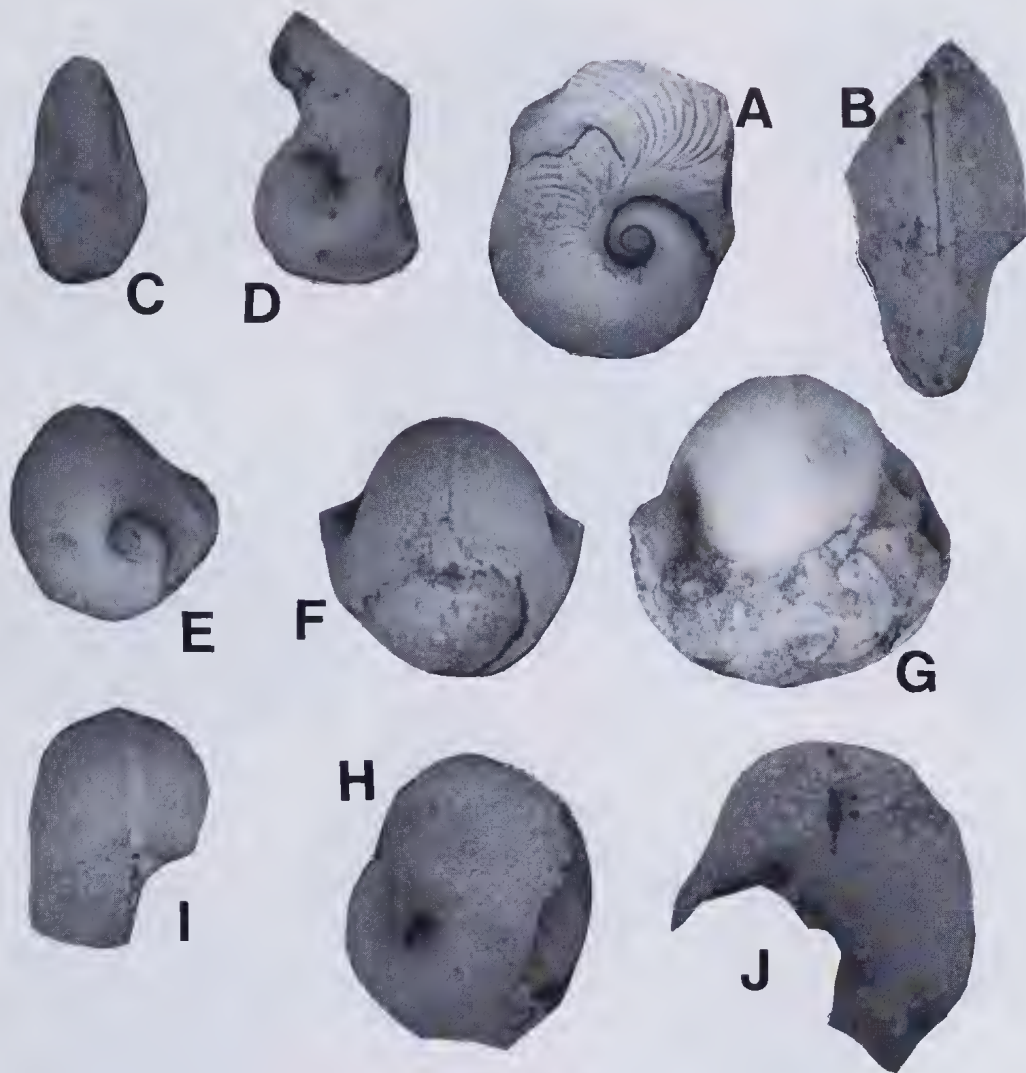


FIG. 1. A-E. *Ningbingia robertsi* gen. et. sp. nov. A, B, Holotype QMF35059. A, x1, B, x1.5. C, D, Paratype QMF35010 x 2. E, Paratype QMF35061 x 1. F-J, *Aglaoglypta veeversi* sp. nov. F, G, H Holotype QMF35539, x 2.5. I, Paratype QMF35540 x 2. J, Paratype QMF35541 x 2.5.

35085, 35094-35098, 35100-35104, 35107, 35109-35115, 35120, 35122-35127 all from QML1035.

DIAGNOSIS. Medium sized, turritiform, medium to high-spined, phaneromphalous with circumbilical nodose cord.

DESCRIPTION. Shell medium-sized to large, turritiform, phaneromphalous, with a variable spire height (Table 3). Sutures impressed, whorls embrace below mid-whorl. In early whorls the whorl profile is rounded, however, in later whorls the whorl profile consists of a sub rounded, shallow sloping subsutural surface bordered abapically by a weak angulation, near vertical slightly

rounded midwhorl, similarly bounded, and a rounded lower whorl profile giving way to an umbilicate base. The umbilicus occupies up to 1/3 of the base and a circumbilical nodose cord is present. Surface of the shell has adhered skeletal fragments on midwhorl, on the angulation on the upper mid whorl or has shallow pits on the mid whorl face. Growth lines are fine, numerous and nearly orthocline. Aperture is quadrate, wider than high with a slight parietal invagination. Early whorls are septate, with a few closely spaced septa in a few specimens. Generally the early whorls are missing.

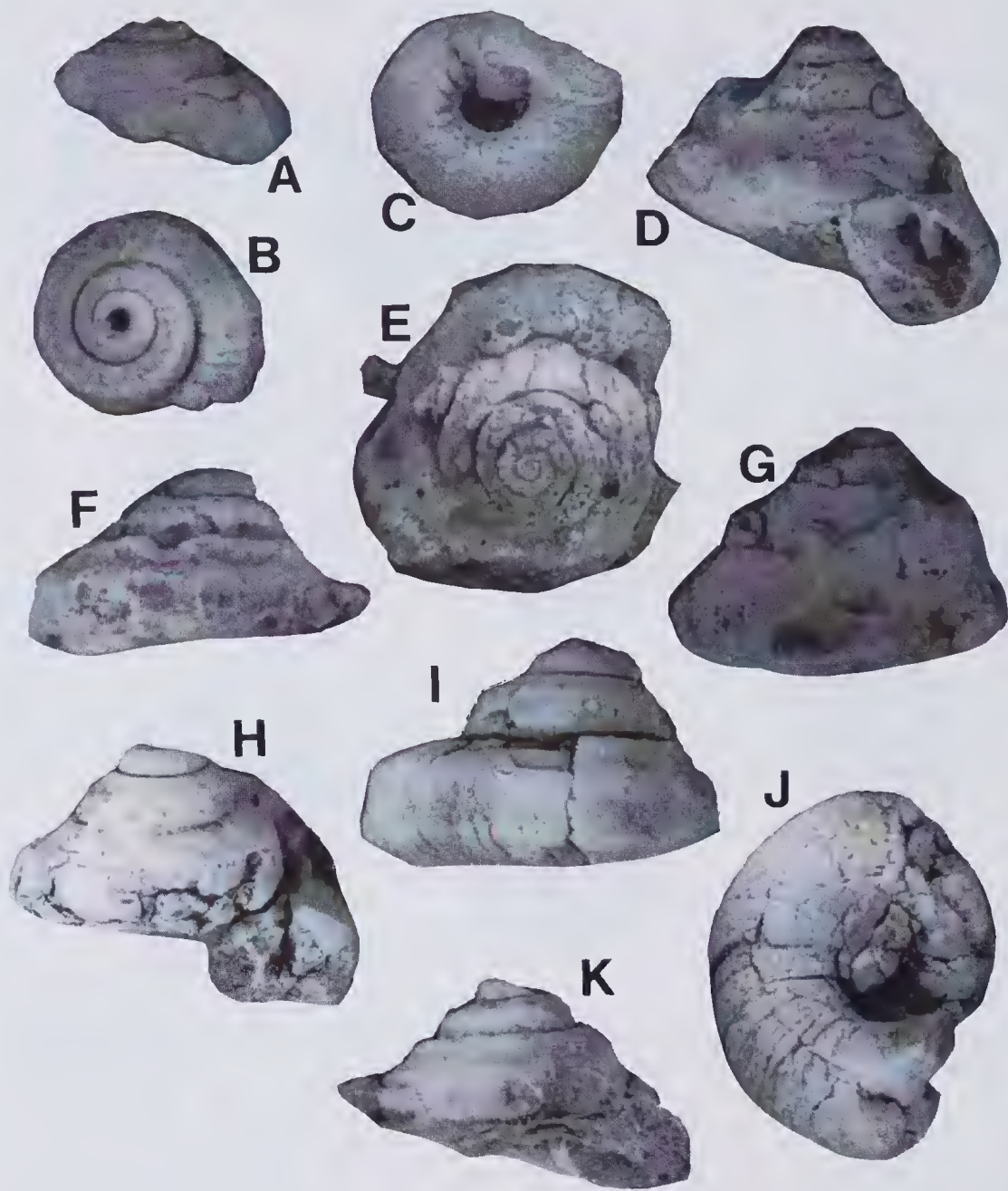


FIG. 2 *Pseudomphalotrochus bonapartensis* sp. nov. A-C, Holotype QMF35087 x1.5. D-G, Paratype QMF35104, x1.8. H-I, Paratype QMF35075 x 1.8. K, Paratype QMF35102 x 1.8.

REMARKS. Blodgett (1992) erected this genus for large gradate omphalotrochids with a circumbilical ridge on the basal angulation. The type species *P. linsleyi* Blodgett, 1992 from the Eifelian of Alaska has a more prominent angulation

on the base, but shares the circumbilical cord. The Bonaparte species is most closely allied with *P. hoffmanni* (Linsley & Yochelson, 1973, from the late Eifelian Rogers City Limestone, Michigan. They share similar whorl profiles, and both have

TABLE 3. Shell measurements for *Pseudomphalotrochus bonapartensis* sp. nov.

Specimen	Height (mm)	Width (mm)
QMF35087	15.0	21.2
QMF35103	19.5	23.0
QMF35081	20.9	22.5
QMF35100	23.6	28.7
QMF35104	17.8	23.0
QMF35125	22.3	27.5

a circumbilical cord, although *P. hoffmanni* lacks nodes on that cord. Also included in *Pseudomphalotrochus* by Blodgett (1992) was *Cirrus leonhardi* D'Archaic & DeVerneuil, 1842, which has a nodose upper whorl angulation. It is impossible to discuss this taxon without reference to closely related species of euomphalids. Linsley & Yochelson (1973) reviewed a number of *Straparollus* taxa including *S. (S.) hoffmanni*, assigned to *Pseudomphalotrochus* by Blodgett (1992), with material adhered to the shell, collectively referring to them as the 'Devonian carrier shells'. Importantly they remarked on the variability in relative spire height in both *S. (Straparollus)* and *S. (Euomphalus)*. The variation in whorl profile present in *P. bonapartensis* is also recorded in *S. (?E.) incrustatus* Linsley & Yochelson, from the Middle Devonian of Utah. It could be argued that this species should be placed in *Micromphalus* Knight, 1945, given the high spire and the angular faces on the whorl profile. However the W.A. specimens have the upper whorl profule sinus, and a wide rather than a narrow umbilicus, a narrow umbilicus being diagnostic for *Micromphalus*. The presence of this genus in faunas of this age is not unexpected and highlights affinities to faunas in North America and Europe.

Suborder INDET.

Superfamily PALAEOTROCHOIDEA Knight, 1956

Family PALAEOTROCHIDAE Knight, 1956

Westwooditrochus gen. nov

ETYMOLOGY. For Westwood Ck, the type locality, and *trochus* referring to the trochiform shell.

TYPE SPECIES. *Westwooditrochus westwoodensis* sp. nov.

DIAGNOSIS. Medium sized, squatly turbini-form, with flattened base, cryptomphalus with callus pad, nodose cord just below suture, another on angulation at whorl periphery situated well below mid-whorl; growth lines opisthocline on upper whorl face.

REMARKS. The lower cord and angulation, combined with the unusual orientation of the growth lines define placement within the family, but the material cannot be accommodated in *Palaeotrochus* Hall, 1879 which lacks the upper cord or *Turbinopsis* Grabau & Shimer, 1909 which not only lacks the upper cord but possesses strong ridges on the upper whorl face. The base of the Bonaparte species is more flattened than other members of the family and possesses an umbilical plug.

Westwooditrochus westwoodensis sp. nov.

(Fig. 3A-F)

ETYMOLOGY. For Westwood Ck, the type locality.

MATERIAL. Holotype: QMF35014. Paratypes: QMF35009, 35011 all from QML1037.

DIAGNOSIS. As for genus.

DESCRIPTION. Shell thick, medium sized, rapidly expanding, squatly turbini-form. Sutures impressed; whorls embrace at periphery which is well below the mid-whorl. Whorl profile angular, with nodose carina at periphery. Upper whorl surface is about 2/3 of the profile, steep (approx. 45°); adjacent to the suture it bears a spiral row of nodes. Below the periphery the lower whorl profile is an inclined surface itself bounded abapically by a weaker nodose spiral cord. Base flattened with an additional, weaker cord near the outer margin. An umbilical pulg occupies more than half of the base. Growth lines are fine and numerous, gently curved and opisthocline on the upper whorl surface, with a slight sinus, nearly straight across the peripheral angulation and strongly prosocline on the base.

Suborder NERITOPSINA Cox & Knight, 1960
Superfamily NERITOIDEA Rafinesque, 1815

Plagiothyra Whidborne, 1892

TYPE SPECIES. *Monodonta purpurea* d'Archaic & de Verneuil, 1842 from the Middle Devonian of Paffrath, Germany.

Plagiothyra curlyjigga sp. nov. (Fig. 4A-G)

ETYMOLOGY. From the vernacular of P.A. Jell for fossil snail; 'curly-jigger'.

MATERIAL. Holotype: QMF35045. Paratypes: QMF35046-35052, 35105, 35106, 35108, 35119, all from QML1035.

DIAGNOSIS. Large member of genus with elongated nodes on the strong spiral ornament.

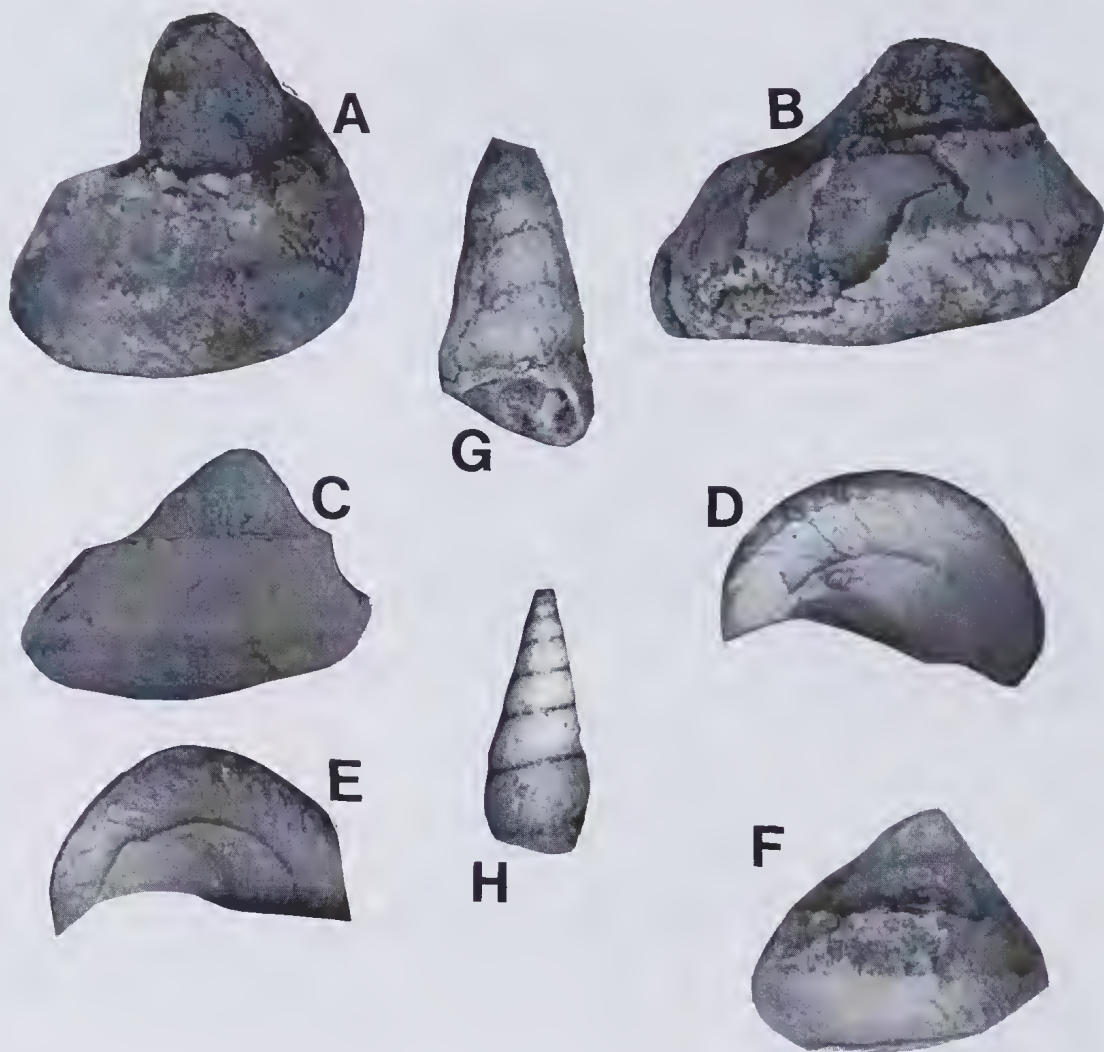


FIG. 3. A-F, *Westwooditrochus bonapartensis* gen. et sp. nov. A, B, Paratype QMF35009 x 1.5. C, D, Holotype QMF35014 x 1.5. E, F, Paratype QMF35011 x 1.5. G, H, Murchisoniidae gen. et sp. indet.; G, QMF35078 x 1.5; H, QMF35093 x 1.5.

DESCRIPTION. High-spired, dextral, turbiniform, thick-shelled and anomphalous. Sutures moderately impressed, whorls embrace just below periphery situated slightly below mid-whorl. Whorl profile rounded with widened mid-whorl area. Whorl face adorned by up to 13 nodose spiral cords. On the holotype the cords are sporadically interrupted such that they possess elongated nodes, presenting a dashed-line appearance. On other specimens the nodes are more rounded. Aperture rounded with invagination near the suture. The holotype possesses a small fold on the upper part of the parietal lip as it approaches the suture. Proto-

conch present on the holotype is simple, smooth and dextral.

REMARKS. The single parietal fold, combined with the strong spiral, nodose ornament places the material in *Plagiothyridae* Knight, 1956. It is most similar to *Plagiothyra* Whidborne, 1892 and is placed there given the singular parietal fold. The type species *Monodonta purpurea* d'Archaic & de Verneuil, 1842, from the Middle Devonian of Paffrath, Germany is only 22mm high, in stark contrast to the Bonaparte species, and the genus lacks the strongly elongated aspect to nodes on the spiral cords. *Dirachis atavus* of Whidborne

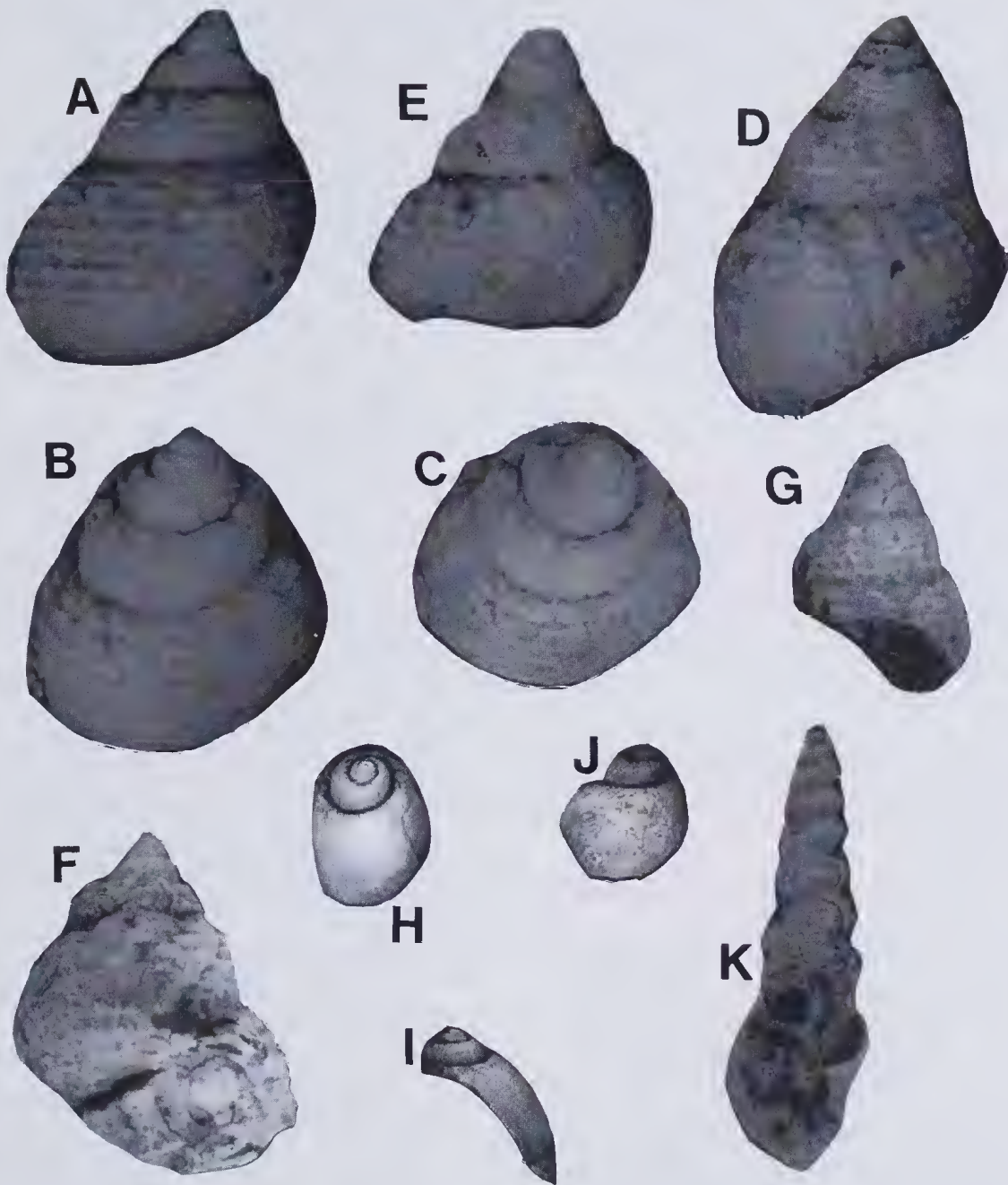


FIG. 4. A-G, *Plagiothyra curlyjigga* sp. nov. A-C, Holotype QMF35045 x 2. D, Paratype QMF35046 x 2. E-F, Paratype QMF35047 x 2. G, Paratype QMF35051 x 2. H-J, *Naticopsis (Naticopsis)* sp. H, I, QMF35013 x 1. J, QMF35109 x 1. K, *Murchisonia (Murchisonia)* sp. QMF35015 x 1.5.

(1892), from the Middle Devonian of Chudleigh is only 13mm high, has similarly elongated nodes on the spiral cords, but possesses two folds on the

inner lip. The species is clearly closely related to both *Dirachis* and *Plagiothyra*.

TABLE 4. Shell measurements for Murchisoniidae gen. et sp. indet.

Specimen	Height (mm)	Width (mm)
QMF35077	22.7	13.5
QMF35078	25	12
QMF35092	14.9	9.5
QMF35093	20	10

Family NERITOPSIDAE Gray, 1847
Subfamily NATICOPSINAE Miller

Naticopsis M'Coy, 1844
Naticopsis (Naticopsis) M'Coy, 1844
Naticopsis (Naticopsis) sp.
(Fig. 4H-J)

MATERIAL. QMF35109, 35538 from QML 1037, QMF35013 from QML1035.

DESCRIPTION. Small to medium sized, naticiform, rapidly expanding shell, maximum height 22mm, maximum width 17mm. Suture strongly impressed, channelled in largest specimen (QMF35013). Whorls embrace high on whorl face. Whorl profile rounded with midwhorl slightly below periphery. Aperture ovate with vertical axis longer. Growth lines very fine, slightly prosocline.

REMARKS. Poor preservation, and the small number of specimens, renders specific diagnosis impossible. The material possesses the characteristic globular form and growth lines of the subgenus.

Suborder MURCHISONIINA Cox & Knight,
1960

Family MURCHISONIIDAE Koken, 1896

Murchisonia d'Archaic & de Verneuil, 1841
Murchisonia (Murchisonia)
d'Archaic & de Verneuil, 1841
Murchisonia (Murchisonia) sp.
(Fig. 4K)

MATERIAL. QMF35015 from QML1037.

DESCRIPTION. A very high-spined, narrow, and multi-whorled shell which is partially weathered from limestone. It is 40.7mm high, with a basal width of 13.6mm. At least 9 whorls present but the apex is obscured. Suture impressed and whorls embrace well below mid whorl. Whorl profile angular with mid-whorl peripheral angulation bearing a selenizone flanked by two cord. A very weak spiral thread is present on the lower whorl surface.

REMARKS. I am unable to nominate a species based on the single poorly preserved specimen.

Murchisoniidae gen. et sp. indet.
(Fig. 3G, H)

MATERIAL. QMF35077, 35078, 35091-93.

DESCRIPTION. Medium-sized, anomphalus, high spired, up to 25mm high and 13.5mm wide (Table 4). Suture weakly impressed. Whorl profile flattened to very weakly rounded. Weak spiral thread present on the lowermost whorl face, just above the suture.

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HEIDECKERNEMA GEN. NOV. A REPLACEMENT NAME FOR THE DEVONIAN TURRETELLID **TRINEMA** COOK. *Memoirs of the Queensland Museum* 42(2): 458. 1998:- *Trinema*, with type species *T. heideckeri* Cook, 1997 was erected for a turretellid gastropod from the Middle Devonian Burdekin Formation. This name is invalid as the generic name is occupied by a thecamoeban protistan *Trinema* Dujardin, 1841. I propose the new name *Heideckernema* to replace *Trinema* Cook, 1997. The name is in honour of Eric Heidecker.

I thank Joan Thorne (Zoological Record) for bringing this oversight to my attention.

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TWO NEW SPECIES OF *RAMPHOTYPHLOPS* (SQUAMATA: TYPHLOPIDAE) FROM QUEENSLAND

PATRICK J. COUPER, JEANETTE A. COVACEVICH AND STEPHEN K. WILSON

Couper, P.J., Covacevich, J.A. & Wilson, S.K. 1998 06 29: Two new species of *Ramphotyphlops* (Squamata: Typhlopidae) from Queensland. *Memoirs of the Queensland Museum* 42(2): 459-464. Brisbane. ISSN 0079-8835.

To Australia's *Ramphotyphlops*-rich herpetofauna are added *R. robertsi* sp. nov. and *R. aspina* sp. nov. The former is known only from the holotype from Shipton's Flat, near Cooktown, northeastern Queensland. A midbody scale count of 22 separates it from all but five of its Australian congeners. From these it is easily distinguished by its strongly dichromatic pattern. *Ramphotyphlops. aspina* sp. nov. is known from the holotype and one paratype from the Barcaldine area, central Queensland. This species is very distinct, lacking the caudal spine which appears to be present in all other Australian *Ramphotyphlops* spp.

□ *Squamata, Typhlopidae, Ramphotyphlops, Queensland, Australia.*

P.J. Couper, J.A. Covacevich & S.K. Wilson, *Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 21 November 1998.*

Australia's snakes are relatively well-known taxonomically and, to a lesser degree, ecologically. However, one family, Typhlopidae, remains poorly-known on both fronts. Relative neglect of Australia's highly diverse *Ramphotyphlops* spp. results from a combination of factors. Many species are small, and similar superficially. Most are grey-brown/brown and have high ventral scale counts and head shields which are difficult to delineate. Hence, examination of specimens is time-consuming. Further, specimens of *Ramphotyphlops* are difficult to collect so, for many species, there are only small series in museum collections. Several species are known only from type material.

To the already *Ramphotyphlops*-rich Australian herpetofauna we add two new, highly-distinctive species. Prior to their discovery, 34 species of *Ramphotyphlops* were recognised from Australia, 16 from Queensland. Most Queensland species were described in the late 19th century in pioneering works by early 'giants' of herpetology (e.g., A. Boulenger, J. E. Gray and G. Peters); two date from the only Australia-wide revision of the genus (Waite, 1918); and two have been described recently (Ingram & Covacevich, 1993). Increasingly, it has become apparent that Australia's tropics and subtropics harbour many undescribed species (e.g., Storr, 1981; Ingram & Covacevich, 1993; Shea & Horner, 1997).

One of the new species is unusual in being markedly dichromatic. The other appears to be unique amongst Australian *Ramphotyphlops* spp. in lacking a caudal spine, a feature regarded as consistently present in the genus (e.g., Cogger,

1994; Storr et al., 1986). Like many other *Ramphotyphlops* spp., both are based on small samples — the first (from near Cooktown, northeastern Queensland [NEQ]) on a single specimen; the second (from the Barcaldine area, central Queensland [CQ]) on two specimens collected close to 80 years apart. While recognising that description of these species from such scant material precludes an account of variation, it seems reasonable to proceed because many more years may elapse before more specimens of either can be located. The collector of the NEQ specimen is a naturalist who has lived near the collection locality for 40+ years and knows the area intimately. That he has seen only one specimen of this species in that time evidences the difficulty in obtaining additional material. The specimens of these new species are small and slightly damaged. To avoid further damage, dissections to determine sex/maturity/state of male genitalia have not been undertaken. We follow Shea & Horner (1997) in assigning these new species to *Ramphotyphlops* on the basis of geography (Robb, 1966).

MATERIALS AND METHODS

Snout-vent length was measured with a standard 30cm ruler. The rostral/head width ratio was calculated from head drawings of the holotypes. All other measurements were taken using Mitutoyo electronic callipers. The species accounts follow the format of Shea & Horner (1997).

The presence of a caudal spine in all currently recognised Australian species (34) except the new species from the Barcaldine area was confirmed by examination of specimens of the species

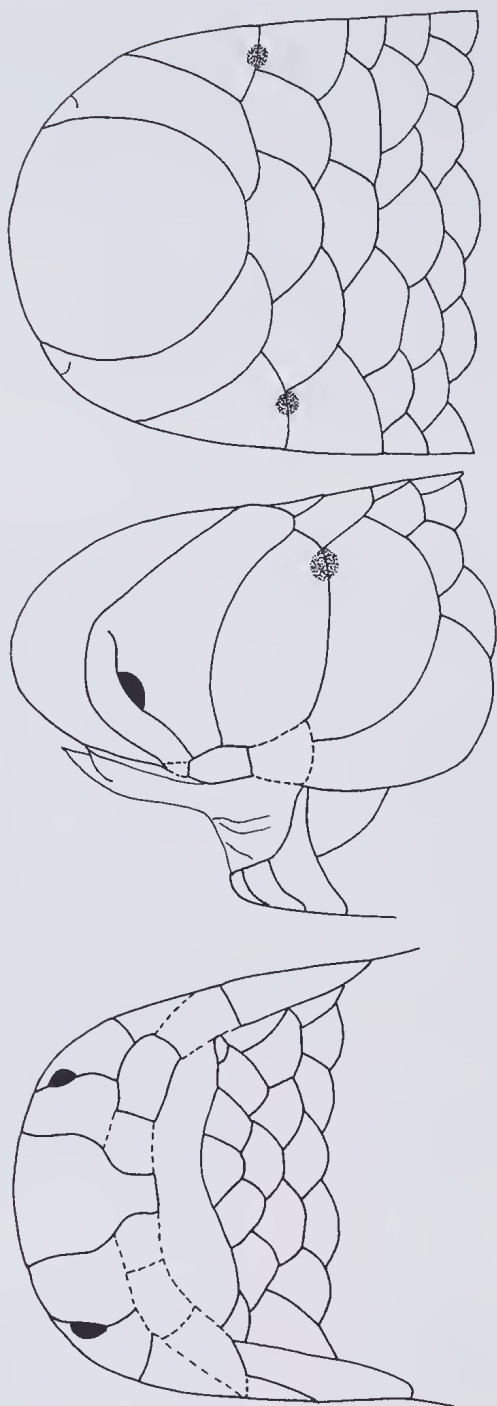


FIG. 1. *Ramphotyphlops robertsi* sp. nov. (Holotype QMJ63736) Above, dorsal view of head. Centre, lateral view. Below, ventral view.

listed in Appendix 1. One type description: *R. toveli* (Loveridge, 1945); extrapolation from Cogger (1986), Storr et al. (1986) and Aplin &

Donnellan (1993): *R. australis* (Gray 1845), *R. centralis* Storr, 1984, *R. endoterus* (Waite, 1918), *R. hamatus* Storr, 1981, *R. howi* Storr, 1983, *R. kimberleyensis* Storr, 1981, *R. leptosoma* Robb, 1972, *R. leucoproctus* (Boulenger, 1889), *R. margaretae* Storr, 1981, *R. micromma* (Kingham, 1929), *R. pilbarensis* Aplin & Donnellan, 1993, *R. pinguis* (Waite, 1897), *R. troglodytes* Storr, 1981, *R. waitii* (Boulenger, 1895) and *R. yampiensis* Storr, 1981. Whether the presence or absence of a caudal spine is related to sexual or ontogenetic differences, or damage, was assessed in a sample of 24 *R. nigrescens* which contained adults of both sexes, and juveniles. All specimens, including those desiccated or damaged, have a prominent caudal spine. Removal of the distal scale containing the caudal spine from one specimen (QMJ57932) required considerable force. Once this was done, the tail of this specimen was compared with those of the two specimens from the Barcaldine area (QMJ7, J51541). The tails of both Barcaldine specimens were intact, being capped by a smooth, highly-polished distal scale. By comparison, the tail of QMJ57932 terminated in dull, dermal tissue.

***Ramphotyphlops robertsi* sp. nov.**
(Figs 1 & 2)

ETYMOLOGY. Named for Lewis Roberts, eminent naturalist and Honorary Consultant of the Queensland Museum, collector of the holotype.

MATERIAL. HOLOTYPE: QMJ63736, Romeo Ck, via Shipton's Flat (15°50'S, 145°14'E) NEQ, 10 Feb, 1983.

DIAGNOSIS. *Ramphotyphlops robertsi* sp. nov. is easily distinguished from its congeners by the following characters combined: strongly dichromatic pattern (in alcohol, dorsum purplish brown, venter white); 22 midbody scale rows; 556 ventrals; a bluntly-rounded snout; rostral circular from above; nasal not completely divided by nasal cleft, just visible from above and joining second supralabial below.

DESCRIPTION. Head smoothly-rounded above and in profile; dorsal surface of rostral large and circular (58% head width); ventral lobe of rostral narrower (32% head width), tapering caudally, lateral margins concave; nasals broadly separated by prefrontal; prefrontal slightly larger than frontal; supraoculars broadly separated by prefrontal/frontal junction; nostrils inferior, near apex of snout, equi-distant from rostral and preocular, opening laterally; nasal cleft beginning at second supralabial, extending across rostroventral margin of nostril, then curving towards the rostral and



FIG. 2. Holotype of *Ramphotyphlops robertsi* (QMJ63736).

terminating $2/3$ the distance from nostril to rostral, just visible from above; preocular narrower than nasal and subequal to ocular; eye small only just visible, beneath preocular/ocular suture, and immediately below preocular/ocular/supraocular junction; posterior edge of ocular overlaps three equal scales (one parietal and two postoculars); four supralabials — first smallest and overlapped by rostral lobe of nasal; second supralabial larger overlapped by rostral lobe and caudal lobe of nasal and preocular; third supralabial larger, overlapped by preocular, strongly overlapping ocular; fourth supralabial much the largest, elongate, overlapped by ocular; mental subequal to postmental; infralabials three — second largest; microtubercles of head shields most dense on nasal scute and lower surface of rostral; glands visible beneath posterior margin of nasals; tail with terminal spine.

Midbody scale rows 22; ventral scales 556; subcaudal scales 12; SVL 285mm; body width 4.3mm (1.5% SVL); tail length 4.7mm (1.6% SVL); head width 2.9mm (1.0% SVL).

Colour in alcohol, strongly dichromatic, dorsal and ventral colours sharply delineated; dorsum dark purplish brown (11 scale rows); rostral cream; venter uniformly cream (11 scale rows).

COMPARISON. *Ramphotyphlops robertsi* can be confused with only *Ramphotyphlops* spp. which have 22 midbody scale rows and a nasal cleft beginning at the second supralabial [from Australia - *R. australis*, *R. hamatus*, *R. kimberleyensis*, *R. pilbarensis*, *R. polygrammicus* and *R. troglodytes*; from PNG/eastern Indonesia - *R. depressus* (Peters, 1880), *R. flaviventer* (Peters, 1864), *R. olivaceus* (Gray, 1845) and *R. willeyi* (Boulenger, 1900)]. It can be separated from the Australian spp. by its strongly dichromatic colour/pattern. *R. robertsi* is further separated from *R. australis* by a considerably higher ventral scale count (556 vs 278-357); from *R. hamatus* and *R. pilbarensis* by snout shape in profile (rounded vs angular); from *R. kimberleyensis* and *R. polygrammicus* by the shape of the rostral from above (circular vs elongate) and from *R. troglodytes* by

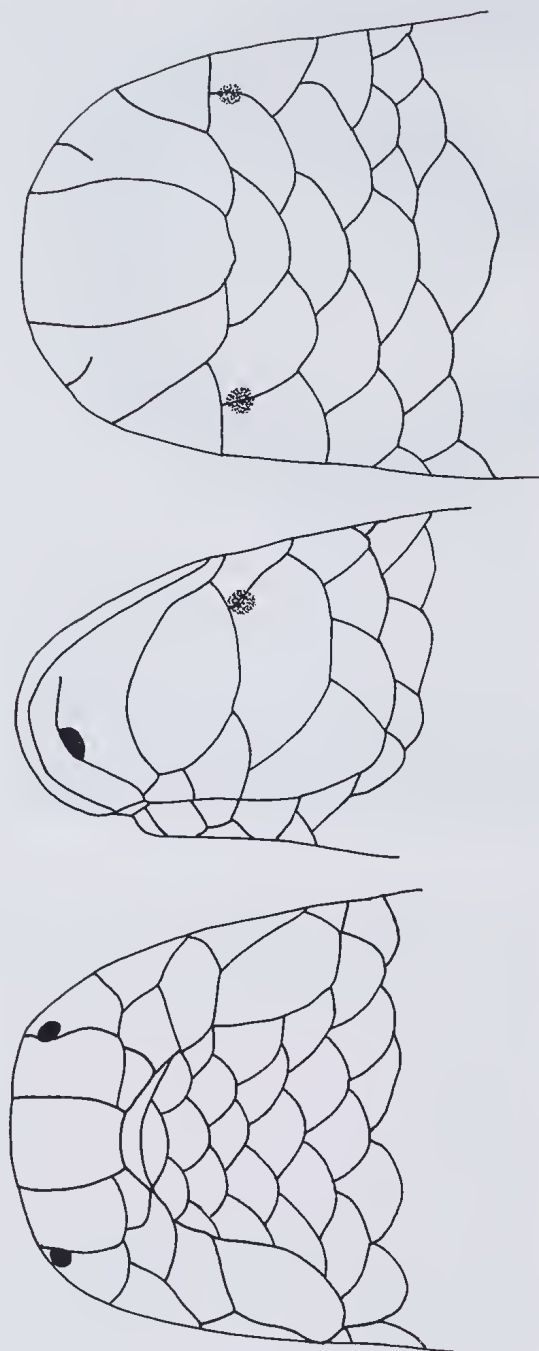


FIG. 3. *Ramphotyphlops aspina* sp. nov. (Holotype QMJ51541). Above, dorsal view of head. Centre, lateral view. Below, ventral view.

the nasal cleft (not completely dividing nasal scale vs completely dividing nasal scale). From the PNG/eastern Indonesia spp. (except *R.*

flaviventer) it can also be separated by its strongly dichromatic colour/pattern. From *R. flaviventer* it is readily distinguished by the shape of the rostral from above (circular vs oval). This character also separates it from *R. depressus*. *R. robertsi* is further separated from these two species by the condition of the nasal cleft (visible from above vs not visible from above); from *R. olivaceus* by its rostral scale (without a transverse keel vs with a transverse keel) and from *R. willeyi* by its snout profile (smoothly-rounded vs a rounded wedge) (McDowell, 1974; Wallach, 1996).

HABITAT. Open forest dominated by Blue Gum, *Eucalyptus tereticornis*, Brown Bloodwood, *E. trachyphloia* and Yellow Stringybark, *E. acmenoides*.

REMARKS. The type specimen was found emerging from a fallen *Eucalyptus* branch which had been hollowed-out by termites, and subsequently recolonised by small black ants. Both the snake and the ants were 'agitated', suggesting that the branch may have fallen to the ground recently. The snake was seen feeding on ant eggs, which were regurgitated after its capture (L. Roberts, pers. comm.).

***Ramphotyphlops aspina* sp. nov.**
(Figs 3 & 4)

ETYMOLOGY. Latin, *a-*, without and *spina*, a spine.

TYPE MATERIAL. HOLOTYPE: QMJ51541, Margot Stn, 20km N Barcaldine (23°27'S, 145°16'E) CQ, donated 1990 by Tim Pulsford. PARATYPE: QMJ7, Coreena Stn, Barcaldine (23°17'S, 145°24'E) CQ, registered 26 May, 1911, donated W.C. Miller.

DIAGNOSIS. *Ramphotyphlops aspina* lacks a caudal spine. It is further distinguished from other members of the genus by the following characters combined: 18 midbody scale rows; 403-428 ventrals; snout bluntly-rounded from above, rounded and flattened laterally; rostral elongate from above; nasal not completely divided by nasal cleft, clearly visible from above and joining second supralabial below.

DESCRIPTION. Head rounded and slightly-flattened in profile; head bluntly rounded dorsally, slightly 'squared'; rostral large and elongate above (37% head width), slightly tapered caudally; ventral lobe of rostral narrower (24% head width) tapering caudally, lateral margins parallel; nasals broadly separated by prefrontal (QMJ51541) or in point contact (QMJ7); prefrontal slightly larger than frontal (QMJ51541) or smaller than frontal (QMJ7); supraoculars broadly separated by prefrontal/frontal junction;



FIG. 4. Holotype of *Ramphotyphlops aspina* (QMJ51541).

nostrils inferior, near apex of snout, equi-distant from rostral and preocular, opening laterally; nasal cleft beginning at second supralabial, extending across rostroventral margin of nostril, passing dorsally and slightly rostrally to terminate 2/3 to 3/4 the distance from nostril to rostral, clearly visible from above; nasal wider than preocular; preocular about as wide as ocular; eye small and distinct beneath ocular/supraocular junction, immediately posterior to preocular/ocular/supraocular junction; ocular caudally overlaps two postoculars and a larger parietal; first supralabial smallest, overlapped by rostral lobe of nasal; second supralabial larger, overlapped by rostral lobe and caudal lobe of nasal and preocular; third supralabial larger, overlapped by preocular but strongly overlapping ocular; fourth supralabial much the largest, elongate, overlapped by ocular; mental narrower than postmental; infralabials three – third the largest; microtubercles of head shields densest on lower surfaces of rostral and nasals; glands not visible below margins of head shields; tail lacking terminal spine.

Midbody scale rows 18; ventral scales 403-428; subcaudal scales 10-16; SVL 230-275mm; body width 3.6-3.7mm (1.3-1.6% SVL); tail length 1.1-2.3% SVL; head width .94-1.1% SVL.

Measurements of holotype: ventral scales 403; subcaudal scales 16; SVL 230mm; body width 3.8mm; tail 5.5mm; head width 2.6mm.

Colour in alcohol, pale pinkish/tan above and below; each scale with a darker edge.

COMPARISON. Only Australian species of *Ramphotyphlops* have 18 midbody scale rows. *Ramphotyphlops aspina* can be confused with those Australian species having 18 midbody scale rows and a nasal cleft beginning at the second supralabial (*R. affinis*, *R. grypus*, *R. guentheri*, *R. howi*, *R. leptosoma*, *R. margaretae*, *R. micromma* and *R. chamodracaena*). It is separated from these species in lacking a caudal spine. *R. aspina* can be separated further from *R. affinis* and *R. grypus* by its snout profile (rounded vs angular); from *R. guentheri*, *R. margaretae* and *R. chamodracaena* by its nasal cleft (clearly visible from above vs

not visible from above) and from *R. howi*, *R. leptosoma* and *R. micromma* by its nasal shield (not completely divided vs completely divided).

HABITAT. The only two collection localities for *R. aspina* are in 'sheep country' of Queensland's central downs. Most of the area in which *R. aspina* was found has been cleared of open eucalypt forest and replaced by introduced pasture grasses.

ACKNOWLEDGEMENTS

We are grateful to Paul Horner (Northern Territory Museum, Darwin) for examining specimens in his care; Ross Sadlier (Australian Museum, Sydney) for providing a listing of AM *Ramphotyphlops* specimens from CQ and NEQ; Glenn Shea (Department of Veterinary Anatomy, University of Sydney) for examining the types of *R. minimus* and *R. yirrikalae*; Tim Pulsford (Queensland Department of Environment) for providing collection details, and Jeff Wright for preparing the photographs. We are indebted to Lewis Roberts for collecting specimen QMJ63736 and bringing it to our attention.

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APPENDIX 1

Specimens of *Ramphotyphlops* examined: Queensland Museum: *R. affinis* (Gray, 1845) - QMJ11630, 5262, 23870, 44501; *R. bituberculatus* (Peters, 1863) - QMJ33377, 33378, 33380; *R. braminus* (Daudin, 1803) - QMJ32880, 32970, 39690; *R. broomi* (Boulenger, 1898) - QMJ2954, 20315, 47503; *R. chamodracaena* Ingram & Covacevich, 1993 - QMJ28082, 31963, 39673, 40233 holotype, 41550, 51980; *R. diversus* (Waite, 1894) - QMJ2943 holotype; *R. grypus* (Waite, 1918) - QMJ23943, 27510, 39596; *R. guentheri* (Peters, 1865) - QMJ2266; *R. ligatus* (Peters, 1879) - QMJ57653, 62775; *R. nigrescens* (Gray, 1845) - QMJ2875, 2884, 3447, 5731, 6636, 7346, 10577, 12348, 20696, 22700, 22706, 35333, 35649, 38527, 43754-55, 43780, 44049, 45255, 46130, 46316, 54538, 54856, 57932; *R. polygrammicus* (Schlegel, 1839) - QMJ5748, 59885, 60625, 61588; *R. proximus* (Waite, 1893) - QMJ2936, 10927, 14212, 38741; *R. silvia* Ingram & Covacevich, 1993 - QMJ8521, 23620, 27387 holotype, 31576, 31577, 31579, 35872, 43785, 46128, 60852; *R. unguistrostris* (Peters, 1867) - QMJ29747, 44502, 56903, 58642; *R. weidii* (Peters, 1867) - QMJ22670, 23965, 43373, 47964. Northern Territory Museum: - *R. minimus* - NTMR7521, 9874. *R. nema* Shea & Horner 1997 - NTMR16047, 21665 holotype, 34110. Australian Museum: *R. minimus** (Kingham, 1929) AMR9692 holotype; *R. yirrikalae* (Kingham, 1942) - AMR12381 holotype.

* The holotype of *R. minimus* possesses a caudal spine. However, one of two additional specimens currently assigned to this taxon in the collection of the Northern Territory Museum lacks a spine (P. Horner, pers. comm.).

TWO NEW SPECIES OF *SAPROSCINCUS* (REPTILIA: SCINCIDAE) FROM QUEENSLAND

PATRICK J. COUPER AND LAUREN D. KEIM

Couper, P.J. & Keim, L.D. 1998 06 29: Two new species of *Saproscincus* (Reptilia: Scincidae) from Queensland. *Memoirs of the Queensland Museum* 42(2): 465-473. Brisbane. ISSN 0079-8835.

Saproscincus basiliscus (Ingram & Rawlinson, 1981), a small skink endemic to the rainforests of eastern Queensland, is a composite of three species. These are readily diagnosed by head scalation (suboculars; contact between second supralabial and lower preocular), measurements (SVL; length of original tail) and body scale counts (midbody and paravertebrals). Two species are restricted to northeastern Queensland — *S. basiliscus* (16°02'S - 19°28'S) and *S. lewisi* sp. nov. (15°04'S - 16°08'S). The third, *S. hannahae* sp. nov., is confined to mideastern Queensland (20°15'S - 21°32'S). Published genetic data show that these distributions are in accord with those of some other vertebrate and invertebrate taxa. □ *Saproscincus hannahae*, *Saproscincus lewisi*, *Scincidae*, rainforests, Queensland.

Patrick Couper & Lauren Keim, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 24 October 1997.

Saproscincus Wells & Wellington, 1984 occurs in moist forest habitats of eastern Australia (Cogger, 1994). It currently contains seven species: *S. basiliscus* (Ingram & Rawlinson, 1981); *S. chalcengeri* (Boulenger, 1887); *S. czechurai* (Ingram & Rawlinson, 1981); *S. mustelinus* (O'shaughnessy, 1874); *S. rosei* Wells & Wellington, 1985; *S. spectabilis* (De Vis, 1888) and *S. tetradactylus* (Greer & Kluge, 1980). Three of these (*S. basiliscus*, *S. czechurai* and *S. tetradactylus*) belong to a distinct 'northern' lineage defined by the following synapomorphies: small size (maximum SVL = 47mm); a peculiar arrangement of nuchal scales; an elevated number of premaxillary teeth (13 or more); and a constant clutch size of two (Greer, 1989).

An examination of *Saproscincus basiliscus* specimens from the collections of the Queensland, Australian and South Australian Museums shows that this species, as currently recognised, contains three morphologically distinct populations, two of which represent undescribed taxa. The nominate form occurs in northeastern Queensland (NEQ) from Roaring Meg Valley (16°02'S, 145°21'E) to Mt Elliot (19°28'S, 146°57'E); one new species occurs from Mt Webb National Park (15°04'S, 145°01'E) to the Cape Tribulation area (16°08'S, 145°27'E) NEQ; the other, from Mt Dryander (20°15'S, 148°33'E) to East Funnel Ck (21°32'S, 149°09'E) mideastern Queensland (MEQ).

MATERIALS AND METHODS

All measurements were taken using Mitutoyo electronic callipers. Supraciliaries, supralabials, infralabials, and subdigital lamellae on the 4th toe were counted on both sides of specimens examined. The following mensural characters have been used: snout-vent length (SVL); axilla to groin (AG); tail length, vent to tip (TL); forelimb, axilla to tip of longest digit (L1); hindlimb, groin to tip of longest digit (L2); head length, tip of snout to anterior margin of ear (HL); head width, measured level with the posterior margin of the parietals (HW); snout, tip to anterior margin of orbit (S); eye to ear, posterior margin of orbit to mid, anterior margin of ear (EE). Premaxillary teeth were counted for QMJ58017 and 62437. Clutch size was recorded for QMJ25137, 25229, 24648, 53481 & 57899-900.

SYSTEMATICS

The new species described here can be assigned to the 'northern' lineage of *Saproscincus* by the following synapomorphies: maximum SVL 50mm (see remarks for *S. basiliscus*); the posterolateral edge of each parietal scale is usually bordered by a nuchal and two temporal scales (in some cases the posterior temporal scale is fused with the nuchal scale); 13 premaxillary teeth; and a constant clutch size of two (Greer, 1989). They are readily separated from *S. tetradactylus* by the number of digits on each forelimb (5 vs 4). From *S. czechurai* they are distinguished by the appearance of the breeding males (breeding colours not pronounced vs side of head and neck jet black



FIG. 1. *Saproscincus hannahae* sp. nov. (paratype, QMJ63911; QM photographic collection, image ref. NU908), Finch Hatton Gorge, Eungella NP, MEQ. (B. Cowell)

with some lighter speckling) and the shape of the snout (rounded vs pointed).

***Saproscincus hannahae* sp. nov.**
(Figs 1 & 2)

Lampropholis basiliscus Ingram & Rawlinson, 1981 (part).

ETYMOLOGY. Named for Hannah Couper.

MATERIAL. HOLOTYPE: QMJ57034, Chelmans Rd, Eungella NP (21°00'S, 148°34'E) MEQ. PARATYPES: Queensland Museum. QMJ57899-901, Mt Dryander (20°15'S, 148°33'E); QMJ57008-10, Vine Ck (20°15'S, 148°32'); QMJ35664, 58017, Mt Dryander (20°15'S, 148°33'E); QMJ49759, Conway NP, 20.17, 148.45; QMJ49709, Conway NP (20°18'S, 148°46'E); QMJ32758, 32760, 32766-71, 32780-83, 32794, Brandy Ck (20°21'S, 148°43'E); 58490, Repulse Ck, Conway (20°23'S, 147°46'E); QMJ57030, Puritan Bay (20°29'S, 148°52'E); QMJ59342-43, 61478-82, 61484-85, 61487-90, Mt Macartney (20°50'S, 148°34'E); QMJ49615, 49712, Eungella NP, Palm Valley Track (20°55'S, 148°30'E); QMJ49755, 63911, Eungella NP, Finch Hatton Gorge (20°55'S, 148°30'E); QMJ49756, Eungella NP (20°55'S, 148°30'E); QMJ56277, small knoll immediately WNW of Mt Ossa township (20°55'S, 148°48'E); QMJ53508, Mt Ossa/Ossa Ck, via Mirani (20°56'S, 148°49'E); QMJ53566-67, 53582-84, 53611-12, Coffee Ck, Mt Jukes, via Mackay (20°59'S, 148°57'E);

QMJ53435-39, St Helens Gap, via Mt Charlton (21°00'S, 148°43'E); QMJ53408-09, 53422-24, Mt Charlton, foothills, via Mt Charlton (21°01'S, 148°44'E); QMJ53481, Mt Blackwood NP, via Mackay (21°02'S, 148°56'E); QMJ32602, 32605, 34000-006, 34036, 34038-40, 34042, 34047, 34062, 34066, 34069, 34092-93, 34095-100, Finch Hatton NP (21°06'S, 148°38'E); QMJ49722, Eungella NP, Palm Valley track (21°09'S, 148°30'E); QMJ51126, 62770, Eungella NP, Broken R (21°10'S, 148°30'E); QMJ57067, Teemurra Ck, 8km S. of Finch Hatton (21°13'S, 148°36'E); QMJ53497, 53601, 53614, 53618-21, E Funnel Ck, 12-15km SW Sarina (21°32'S, 149°09'E). Australian Museum. AMR47868, Box Ck, Mt Dryander (20°14'S, 148°31'E); AMR87087-95, 9.15km W of Cathu SF office (20°51'S, 148°38'); AMR87096, 7.4km E of Rd to Mandalay, via Airlie Beach-Shute Harbor Rd (20°17'S, 148°47'E); AMR87097-103, St Helen's Gap, 3.7km N of Mt Charlton by Rd (21°00'S, 148°42'E); AMR111572, Broken R, Eungella NP (21°10'S, 148°30'E). All localities are in MEQ.

DIAGNOSIS. *Saproscincus hannahae* sp. nov. can be confused only with *S. lewisi* sp. nov. and, to a lesser degree, with *S. basiliscus*. It does not occur in sympatry with either species. It can be distinguished from the former by its smaller size (max SVL = 38.4mm vs 42.3mm); length of the original tail (mean 130% SVL vs 161% SVL);

and the arrangement of the second supralabial and lower preocular scales (overlapping and in contact [Fig. 2] vs not in contact, 85% of specimens examined, or only in point contact).

From *S. basiliscus* it is distinguished by its paravertebral count (42-49 vs 50-59); subocular scalation (continuous series of subocular scales in contact with granules of lower eyelid always absent vs only rarely absent (Fig. 3), 3% of specimens examined); smaller size (max SVL = 38.4mm vs 49.8mm); length of original tail (mean 130% SVL vs 163% SVL), and midbody scale count (mean 22 vs 26).

DESCRIPTION. SVL (mm) 17.7-38.35 (mean = 32.3, N = 109). Proportions, (%SVL): AG = 41.4-56.6 (mean = 49.1, N = 100); TL = 113.2-146.6 (mean = 130.0, N = 29); L1 = 24.6-33.3 (mean = 28.9, N = 100); L2 = 34.0-45.5 (mean = 39.3, N = 100); HW = 12.8-16.7 (mean = 14.6, N = 100); HL = 20.4-27.0 (mean = 22.5, N = 100); S = 8.2-11.1 (mean = 9.7, N = 100); EE = 6.7-10.4 (mean = 8.5, N = 100). Nasals widely spaced, rostral and frontonasal in broad contact; prefrontals narrowly to moderately separated; maximum length of frontal 1.2-1.7 × maximum width (mean = 1.5, N = 101); frontal contacting frontonasal, prefrontals, first two supraoculars and frontoparietals; supraoculars 4, second the largest; supraciliaries 6-8 (mean = 7.1, N = 205), first the largest; frontoparietals paired (rarely fused, or partially fused) and distinct from interparietal; enlarged nuchal scales 0-3; loreals 2; preoculars 2, the lower being the largest; presuboculars 2, the first being the largest; supralabials 6-7 (mean = 6.05, N = 212), fourth subocular when six, fifth subocular when seven; infralabials 5-6 (mean = 5.99, N = 211); postmental contacting two infralabials on each side; palpebral disc moderate, less than half the lower eyelid; ear opening small, round or vertically elliptic.

Midbody scale rows 20-24 (mean = 22.3, N = 114); number of scales in a direct line from mental to anal (inclusive) 48-57 (mean = 52.7, N = 75); paravertebral scales, from anterior-most nuchal to posterior margin of hindlimb 42-49 (mean = 47.0, N = 117); lamellae beneath fourth toe 16-22 (mean = 18.6, N = 195), with a medial groove on distal portion. Dorsal surface: fawn to reddish brown. Some scales with dark spots, forming broken, longitudinal lines on back. Lateral surface: flanks paler, weakly to heavily marked by dark flecks arranged in longitudinal rows. Sides clearly demarcated from dorsal surface by a prominent dorsolateral zone which runs as a broad brown bar between

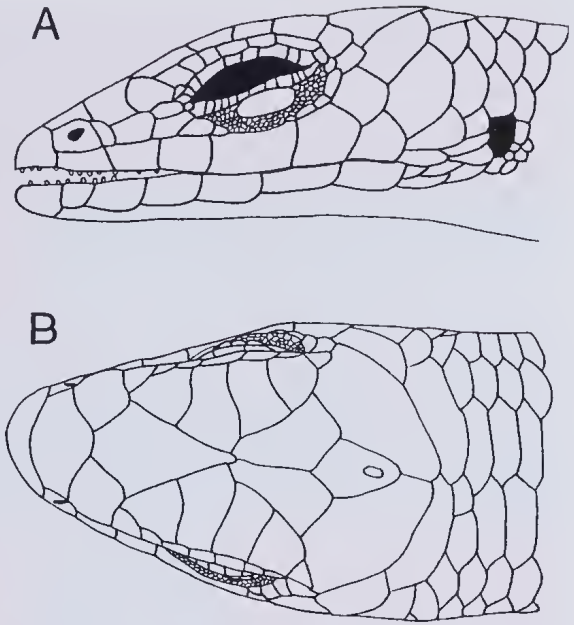


FIG. 2. Holotype of *Saproscincus hannahae* sp. nov. (QMJ57034). A, lateral view of head; B, dorsal view of head.

the eye and forelimb, then breaks into a row of dark spots along the upper flanks. In some specimens, this zone is bordered dorsally by a fine pale stripe. The sides merge evenly with the ventral colours. A distinct light spot is present at the posterior base of the thigh. Ventral surface: white, with dark flecks on throat and tail. Lower surfaces of hands and feet pale brown or whitish. Head: conspicuously marked by dark spots, which begin between the eyes and spread posteriorly to form a 'V' shaped marking on the frontoparietal and parietal scales. Lips barred.

The measurements and scale counts for the holotype (QMJ57034) are as follows: SVL = 33.68mm, AG = 17.34mm, TL = 49.37mm, L1 = 9.39mm, L2 = 13.77mm, HW = 4.94mm, HL = 7.69mm, S = 3.30mm, EE = 2.69mm. Maximum length of frontal 1.4 × maximum width; supraciliaries 7; enlarged nuchal scales 2; supralabials 6; infralabials 6; midbody scale rows 22; number of scales in a direct line from mental to anal (inclusive) 54; paravertebral scales 48; lamellae beneath fourth toe 20/18.

DISTRIBUTION. Confined to rainforests of the Central Mackay Coast Biogeographic region (as defined by Stanton & Morgan, 1977). The broad distribution for this species extends from Mt Dryander, via Proserpine (20°15'S, 148°33'E) to E Funnel Ck, via Sarina (21°32'S, 149°09'E) MEQ.

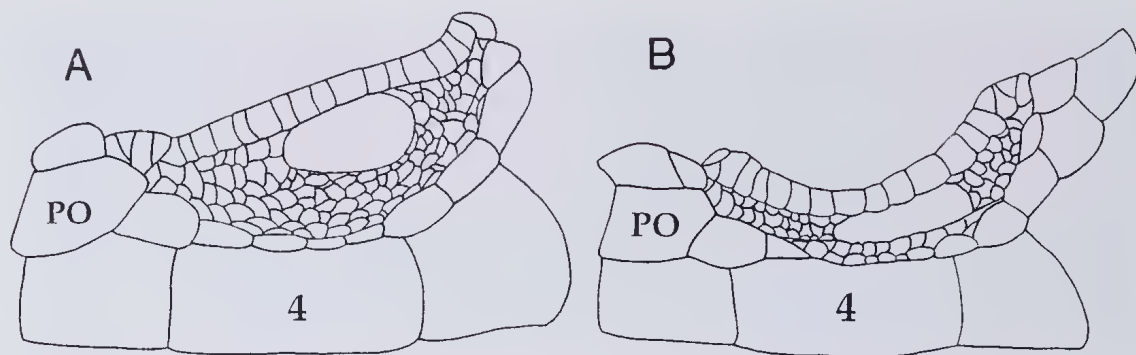


FIG. 3. Variation in the subocular scales of *Saproscincus basiliscus*. A, a continuous series of enlarged subocular scales, holotype (QMJ34409); B, enlarged subocular scales fail to meet beneath the orbit (QMJ52830). PO = preocular, 4 = 4th supralabial.

Disjunct populations occur at Mt Dryander (20°15'S, 148°33'E), Conway Ra. (20°27'S, 148°44'E), Clarke Ra. (21°10'S, 148°30'E), Mt Ossa/Mt Charlton area (21°00'S, 148°43'E), Mt Jukes (21°02'S, 148°57'E), Mt Blackwood (21°02'S, 148°56'E) and in the Connors Ra. (21°32'S, 149°12'E) (Fig. 4).

HABITAT. Complex notophyll and mesophyll vine forests.

HABITS. A secretive litter-skink which always remains close to cover. This species appears to be most common along creek margins.

CONSERVATION STATUS. Specimens of *S. hannahae* sp. nov. have been collected at more than 20 rainforest sites in coastal MEQ (20°15'S - 21°32'S). This species is common and well represented in existing reserves.

REMARKS. Recognition of *S. hannahae* sp. nov. is of note zoogeographically. Prior to the separation of *S. hannahae* from '*S. basiliscus*' sensu lato, the latter was the only reptile 'species' to span the 'Burdekin Gap' — the dry corridor which has separated faunas of NEQ (Wet Tropics Biogeographic Region) and MEQ (Central Mackay Coast Biogeographic Region) rainforest 'islands' for between one million years (e.g., three bird spp., Joseph et al., 1993) and, it is estimated, seven million years [e.g., *Saltuarius cornutus* (Ogilby, 1892)/*S. salebrosus* (Covacevich, 1975), C. Schneider, in press]. Thus, description of *S. hannahae* brings to six [*Phyllurus isis* Couper et al., 1993; *Phyllurus neptus* Couper et al., 1993; *Phyllurus ossa* Couper et al., 1993; *Eulamprus amplus* (Covacevich & McDonald, 1980); *Eulamprus luteilateralis* (Covacevich & McDonald, 1980) and *S. hannahae*],

the number of obligatory rainforest reptile species confined to the Central Mackay Coast.

Ingram & Rawlinson (1981) recognised differences between the populations of *S. basiliscus* (as *Lampropholis basiliscus*) occurring in MEQ and NEQ. While the two populations were similar in colour, pattern and aspects of scalation, the MEQ specimens had a 'tendency to be slightly smaller

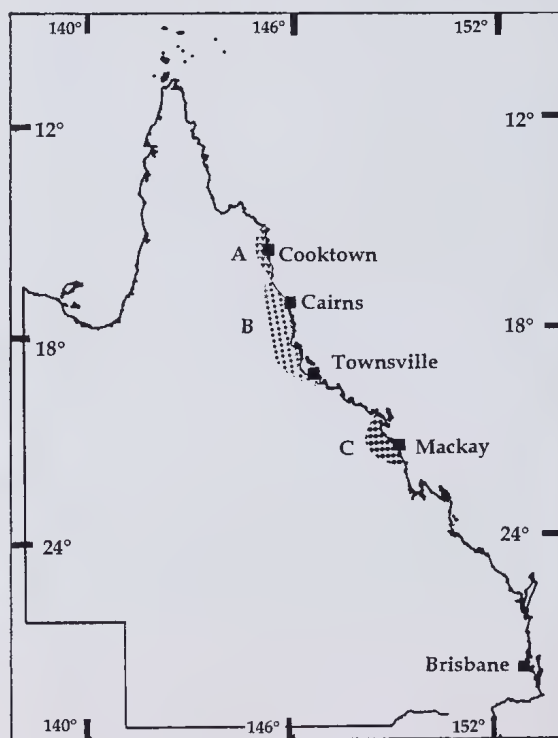


FIG. 4. Map of Qld showing the broad distributions of *S. lewisi* sp. nov. (A), *S. basiliscus* (B) and *S. hannahae* sp. nov. (C).



FIG. 5. *Saproscincus lewisi* sp. nov. (holotype, QMJ62440; QM photographic collection, image ref. NQ819), Shipton's Flat, NEQ. (J. Wright)

and "stubbier", and to have slightly lower mid-body and toe lamellae counts'. They regarded these differences as clinal, rather than warranting specific or subspecific recognition. Consequently, specimens of *S. hannahae* were included in the type series of *L. basiliscus*. The following specimens are paratypes of both species: QMJ32602, 32605, 32758, 32760, 32766-71, 32780-3, 32794, 34000-006, 34036, 34038-40, 34042, 34047, 34062, 34066, 34069, 34092-3, 34095-100. AMR47868, 87087-103.

***Saproscincus lewisi* sp. nov.**
(Figs 5 & 6)

Lampropholis basiliscus Ingram & Rawlinson, 1981 (part).

ETYMOLOGY. Named for Lewis Roberts, an Honorary Consultant of the Queensland Museum.

MATERIAL. HOLOTYPE: QMJ62440 (ethanol preserved), Parrot Ck, Shipton's Flat (15°48'S, 145°15'E) NEQ. PARATYPES: Queensland Museum. QMJ32354-55, Mt Webb NP (15°04'S, 145°07'E); QMJ24648, Helenvale, 13km S, Three Jims Ck, Bloomfield Rd (15°42'S, 145°17'E); QMJ60889, Big Tableland (15°43'S, 145°17'E); QMJ60887, O'Keefe Ck, Big Tableland (15°42'S, 145°16'E); QMJ24918, Home Rule, Slaty Ck, on banks (15°44'S, 145°18'E);

QMJ25137-38, Home Rule to Intake Falls, Home Rule S of Cooktown (15°44'S, 145°17'E); QMJ25229, 25308, Home Rule (15°44'S, 145°17'E); QMJ25257, Home Rule, nr Home Rule Camp, 30km S Cooktown (15°44'S, 145°17'E); QMJ25265, Mt Hedley slopes (15°44'S, 145°16'E); QMJ25289, Home Rule, nr, on Track to Granites (15°44'S, 145°18'E); QMJ25204, Granite Ck to Cedar Bay, on track (15°45'S, 145°20'E); QMJ24848, Mt Hartley, nr Home Rule, S of Cooktown (15°46'S, 145°19'E); QMJ17902, 62432-39, 62461, Shipton's Flat, 38km S Cooktown (15°48'S, 145°15'E); QMJ17903, Shipton's Flat, 32-48km S Cooktown (15°48'S, 145°16'E); QMJ27135, 27141, Shipton's Flat, Site 36 (15°48'S, 145°16'E); QMJ25301, 12 Mile Scrub, 60-121m, Gap Ck (15°50'S, 145°19'E); QMJ27258 12 Mile Scrub, Gap Ck, ca. 30km S Cooktown (15°51'S, 145°21'E); QMJ39436, Bloomfield (15°57'S, 145°20'E); QMJ49599, Roaring Meg R flats, China Camp, via Bloomfield (16°02'S, 145°18'E); QMJ41514, Cape Tribulation, 2.5km W (16°05'S, 145°27'E); QMJ42311, Cape Tribulation (16°05'S, 145°29'E); QMJ49547, Monkhouse Oliver, Mosaic Ck, TR165, Cape Tribulation area (16°12'S, 145°25'E). Australian Museum. AMR26833, Big Tableland (15°43'S, 145°17'E); AMR26783, Home Rule, Slaty Ck, on banks (15°44'S, 145°18'E). South Australian Museum.

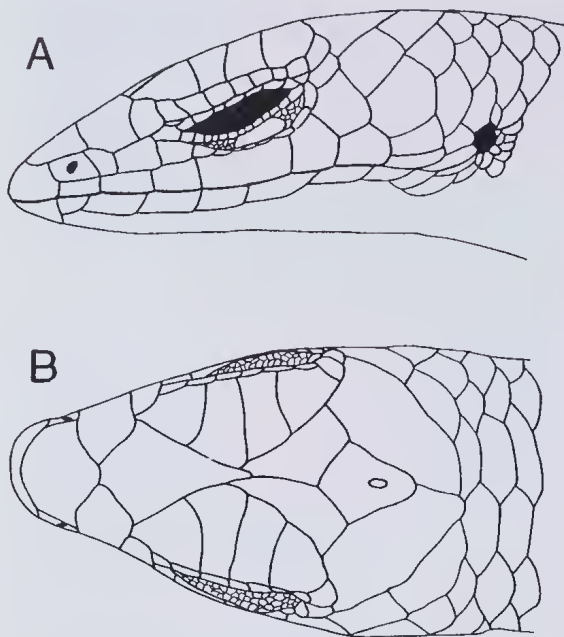


FIG. 6. Holotype of *Saproscincus lewisi* sp. nov. (QMJ62440). A, lateral view of head; B, dorsal view of head.

SAMR9770, Big Tableland (15°43'S, 145°17'E). All localities are in NEQ.

DIAGNOSIS. *Saproscincus lewisi* can be confused with only *S. hannahae* sp. nov. and, to a lesser degree, with *S. basiliscus*. Of these, it is geographically isolated from *S. hannahae*, and may occur in sympatry with *S. basiliscus* in the vicinity of Roaring Meg (16°02'S, 145°21'E) and Cape Tribulation (16°08'S, 145°27'E). It can be distinguished from the former by its larger size (max SVL = 42.3mm vs 38.4mm); length of the original tail (mean 161% SVL vs 130% SVL), and the arrangement of the second supralabial and lower preocular scales (not in contact, 85% of specimens examined [Fig. 6], or only in point contact vs overlapping and in contact).

From *S. basiliscus* it is distinguished by its smaller size (max SVL 42.3mm vs 49.8); paravertebral count (46-50 vs 50-59); and midbody count (mean 22 vs 26).

DESCRIPTION. SVL(mm) 23.48-42.34 (mean = 35.6, N = 39). Proportions, (%SVL): AG = 44.3-54.2 (mean = 47.6, N = 38); TL = 147.5-173.8 (mean = 160.6, N = 8); L1 = 26.7-33.3 (mean = 30.3, N = 38); L2 = 36.5-44.1 (mean = 41.1, N = 38); HW = 11.8-16.9 (mean = 13.9, N = 37); HL = 20.7-25.5 (mean = 22.7, N = 38); S = 8.4-11.3

(mean = 9.7, N = 38); EE = 7.4-9.7 (mean = 8.3, N = 38). Nasals widely spaced, rostral and frontonasal in broad contact; prefrontals narrowly to moderately separated; maximum length of frontal 1.2-1.6 × maximum width (mean = 1.5, N = 38); frontal contacting frontonasal, prefrontals, first two supraoculars and frontoparietals; supraoculars 4, second the largest; supraciliaries 5-8 (mean = 6.8, N = 78), first the largest; frontoparietals paired and distinct from interparietal; enlarged nuchal scales 0-2; loreals 2; preoculars 2, the lower being the largest; presuboculars 2, rarely 1, the first being the largest (mean = 1.98, N = 78); supralabials 6-7 (mean = 6.1, N = 78), fourth subocular when six, fifth subocular when seven; infralabials 5-6 (mean = 5.9, N = 78); postmental contacting 1-2 infralabials on each side (mean = 1.96, N = 78); palpebral disc moderate, less than half the lower eyelid; ear opening small, round or horizontally elliptic.

Midbody scale rows 22-24 (mean = 22.4, N = 39); number of scales in a direct line from mental to anal (inclusive) 52-59 (mean = 53.8, N = 37); paravertebral scales, from anterior-most nuchal to posterior margin of hindlimb 46-50 (mean = 47.9, N = 39); lamellae beneath fourth toe 19-25 (mean = 22.2, N = 71), with a medial groove on distal portion.

Dorsal surface: bronze to mid-brown with a few scattered, dark flecks. **Lateral surface:** flanks uniform brown, or marked with dark flecks arranged in longitudinal rows. Sides often sharply demarcated from dorsal surface by a prominent dorso-lateral zone which runs as a broad brown bar between the eye and forelimb, then continues as a fine line along the upper flanks, or breaks into a row of dark flecks. In some specimens, this zone is bordered dorsally by a fine pale stripe. The sides merge evenly with the ventral colours. A distinct light spot is present at the posterior base of the thigh. **Ventral surface:** white, with dark flecks on throat and tail, and occasionally on the belly. Lower surfaces of hands and feet pale brown or whitish. **Head:** marked by dark and pale spots. These sometimes form a weak 'V' shaped marking on the frontoparietal and parietal scales. Lips barred.

Measurements and scale counts for the holotype (QMJ62440) are as follows: SVL = 34.74mm, AG = 15.55mm, TL = 60.15mm, L1 = 11.58mm, L2 = 15.59mm, HW = 4.81mm, HL = 8.20mm, S = 3.57mm, EE = 3.07. Maximum length of frontal 1.5 × maximum width; supraciliaries 7/8; enlarged nuchal scales 1; supralabials 6; infralabials 6; midbody scale rows 22; number of scales in a direct line from mental

TABLE 1. A comparison of the measurements and scale counts from De Vis' (1888) description of *Mochoa spectabilis* with those of each of the putative 'syntypes'.

	<i>S. spectabilis</i>		<i>S. basiliscus</i>		
	De Vis	J244	J255	J19742	J19743
Total length (mm)	133	133	88.01	10.5	103.4
Head length (mm)	10.5	10.5	9.4	8.3	6
Head width (mm)	6	6	5.9	5	5.2
Body (mm)	42	39.7	33.7	29.7	32.4
Fore Limb (mm)	10.5	13.3	14.7	11.7	12.8
Hind limb (mm)	18	18.3	10.5	16.1	17.5
Tail (mm)	81.5	82.8	44.91	11.5	62
Supraciliaries	7	7	7	7	7
Midbody rows	22	22	28	28	26
Subdigital lamellae (4th toe)	20-24	23-25	21-23	19-20	20

to anal (inclusive) 52; paravertebral scales 48; lamellae beneath fourth toe 23/25.

DISTRIBUTION. From Mt Webb NP (15°04'S, 145°07'E) to the Cape Tribulation area (16°08'S, 145°27'E), NEQ (Fig. 4).

HABITAT. Complex notophyll vine forests.

HABITS. A secretive litter-skink which always remains close to cover. This species appears to be most common along creek margins.

CONSERVATION STATUS. Specimens of *S. lewisi* sp. nov. have been collected at more than 20 rainforest sites in coastal NEQ (15°04'S - 16°08'S). This species is common and well represented in existing reserves.

REMARKS. *Saproscincus lewisi* sp. nov., ranges from Mt Webb (15°04'S, 145°07'E) to Cape Tribulation (16°08'S, 145°27'E) NEQ, *S. basiliscus* from Roaring Meg (16°02'S, 145°21'E) to Mt Elliot (19°28'S, 146°57'E) NEQ, so there is at least a 15km zone of sympatry for these two species. The former is largely 'northern' and the latter largely 'southern' in relation to what has been termed the 'Black Mountain Barrier' (a low, discontinuity in the mesothermal rainforests of the uplands — near Kuranda, 16°49'S, 145°38'E, NEQ), a zone of separation for many obligatory rainforest species of snails, frogs, lizards and birds (Moritz et al., 1996). For the frogs and reptiles at least, this separation is in the order of 2-6 million years, based on genetic studies on: *Litoria genimaculata* (Horst, 1883); *Litoria nanotis* (Andersson, 1916); *Litoria rheocola* Liem,

1974; *Carphodactylus laevis* Günther, 1897; *Saltuarius cornutus* (Ogilby, 1892); and *Gnypetoscincus queenslandiae* (De Vis, 1890) (Schneider et al., in press). The most likely explanation for sympatry of *S. lewisi* and *S. basiliscus* is secondary contact, following reconnection of rainforests.

Ingram & Rawlinson (1981) included specimens of *S. lewisi* in the type series of *S. basiliscus* (as *L. basiliscus*). The following specimens are paratypes of both species: QMJ17902-03, 24648, 24848, 24918, 25137-8, 25204, 25229, 25257, 25265, 25289, 25301, 25308, 27135, 27141, 27258, 32354. AMR26783, 26833.

Saproscincus basiliscus (Ingram & Rawlinson, 1981) sensu stricto

DIAGNOSIS. With the recognition of *S. hanna-hae* sp. nov. and *S. lewisi* sp. nov., the following changes apply to the description of *S. basiliscus*: SVL = 20.14-49.79mm (mean = 38.6, N = 257). (% SVL) T = 141.9-186.5 (mean = 163.0, N = 39); L2 = 36.5-48.4 (mean = 42.9, N = 247).

Midbody scale rows 22-29 (mean = 25.9, N = 254); Paravertebral scale rows 50-59 (mean = 53.5, N = 255); Subocular scales enlarged and continuous 61% (Fig. 3A); small (distinctly larger than granules of lower eyelid) continuous 36%; enlarged suboculars not forming a continuous series beneath eye 3% (N = 259) Fig. 3B. For material examined see Appendix 1.

DISTRIBUTION. Broad distribution for this species extends from Roaring Meg (16°02'S, 145°21'E) to Mt Elliot (19°28'S, 146°57'E), NEQ (Fig. 4).

CONSERVATION STATUS. Throughout most of its range, *S. basiliscus* is a common species that is well represented in existing reserves. However, its status north of the 'Black Mountain Barrier' (16°49'S, 145°38'E) is difficult to assess from existing collections.

REMARKS. The definition provided by Greer (1989) for the 'northern' lineage of *Saproscincus* requires the following change to maximum SVL: 50mm (previously 47mm).

There has been some confusion regarding the type series of *M. spectabilis* De Vis, 1888. Covacevich (1971) identified four syntypes (QMJ244, 255, 19742-3) for this taxon. Subsequent authors followed her interpretation of the type material (Cogger et al., 1983; Wells & Wellington, 1985; Sadlier et al., 1993). Sadlier et al. (1993) found the syntypes to be composite, consisting of one *Saproscincus galli* Wells & Wellington, 1985 (QMJ244) and three *S. basilis-*

TABLE 2. A comparison of the paravertebral scale counts, and the presence (Y) or absence (N) of a continuous series of enlarged subocular scales for the types of *L. basiliscus* (QMJ3449), *S. hannahae* (QMJ57034), *S. lewisi* (QMJ62440) and the putative types of *M. spectabilis*. * = one side only.

Taxa	Paravertebrals	Suboculars
Types		
<i>L. basiliscus</i>	55	Y
<i>S. hannahae</i>	48	N
<i>S. lewisi</i>	48	Y
Putative types		
<i>M. spectabilis</i>		
QMJ244	54	N
QMJ255	57	Y
QMJ19742	56	Y
QMJ19743	54	Y*

cus (QMJ255, 19742-3). They concluded that the designation of QMJ19743 as the lectotype of *M. spectabilis* by Wells & Wellington (1985) meant '...that *Mocoo spectabilis* becomes a senior synonym of, and the available name for the taxon previously known as *Saproscincus basiliscus*'. This interpretation was refuted by Ingram (1994) who argued that De Vis' description of *M. spectabilis* was based on a single specimen (QMJ244). He concluded that '...*Mocoo spectabilis* is a senior synonym of the taxon previously known as *Saproscincus galli* Wells & Wellington, 1985 ... Also, *S. basiliscus* (Ingram & Rawlinson, 1981) remains valid'. We concur with Ingram (1994). Re-examination of the putative type/s for *M. spectabilis* confirms that QMJ244 was, at the very least, paramount in De Vis' (1888) description (Table 1).

Re-examination of the syntypes of *M. spectabilis* (QMJ255, 19742 and 19743) shows that these specimens agree in all respects with *S. basiliscus*. They can be assigned readily to the nominate form by their paravertebral scale counts and the presence of an enlarged series of subocular scales (Fig 3A, Table 2). The collection locality associated with these specimens (Gympie) is obviously in error.

ACKNOWLEDGEMENTS

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APPENDIX 1

Specimens of *Saproscincus basiliscus* examined in this study (259). Queensland Museum. QMJ58441, Roaring Meg Valley (16°02'S, 145°21'E); QMJ60732-33, Thornton Peak, N on Crib track from Daintree R. (16°06'S, 145°20'E); QMJ41727, Mt Ilemant, 6km SW Cape Tribulation (16°07'S, 145°25'E); QMJ43915, Hilda Ck, Thornton Peak, base (16°10'S, 145°23'E); QMJ49696 Oliver Ck, nr road crossing (16°12'S, 145°25'E); QMJ54323, Mt Molloy, 3km N (16°39'S, 145°20'E); QMJ52928, Kuranda (16°49'S, 145°38'E); QMJ55741, Kuranda (16°49'S, 145°38'E); QMJ61037, Saddle Mtn (16°49'S, 145°40'E); QMJ39429, Kuranda, 6km SE (16°52'S, 145°40'E); QMJ39430-31, 39433, Kuranda, 6km SE (16°52'S, 145°40'E); QMJ51951, NorthSouth Bell Peak Saddle, Malbon Thompson Ra (17°06'S, 145°54'E); QMJ48274-76, Danbulla SF, Kauri Ck, Mt Haig Rd (17°07'S, 145°38'E); QMJ48224, Danbulla SF, 1.5km along Kauri Rd (17°08'S, 145°37'E); QMJ12145, Atherton Tblld, Tinaroo Dam (17°10'S, 145°33'E); QMJ49548, Severin, Boar Pocket (17°11'S, 145°40'E); QMJ61041, Danbulla Sci. Res. (17°12'S, 145°4'E); QMJ49711, Gadgarra SF (17°16'S, 145°4'E); QMJ49733, Gadgarra SF (17°16'S, 145°41'E); QMJ12158, L Eacham (17°17'S, 145°37'E); QMJ49702, L Eacham (17°17'S, 145°37'E); QMJ49708, L Eacham NP (17°17'S, 145°37'E); QMJ61038, Graham Range (17°17'S, 145°58'E); QMJ39867-68, Bellenden Ker Ra, 0.5km S Cable Tower No 7 (17°2'S, 145°52'E); QMJ45920, Malanda (17°21'S, 145°36'E); QMJ39866, Bellenden Ker Landing, Russell R at landing (17°22'S, 145°58'E); QMJ45917, Russell R, cave site (17°22'S, 145°53'E); QMJ61040, Upper Plath Rd (17°23'S, 145°28'E); QMJ59161 Topaz, Westcott Rd (17°24'S, 145°41'E); QMJ47931-32, 47960, Mt Bartle Frere (17°24'S, 145°49'E); QMJ49700, Russell R, headquarters (17°24'S, 145°46'E); QMJ12146-47, 49704, 49710, Crater, Atherton Tblld (17°26'S, 145°29'E); QMJ49703, 49706, Boonjee, 6.5km ESE Lammers Hill (17°26'S, 145°46'E); QMJ59121, Hughes Road, Topaz (17°26'S, 145°42'E); QMJ59659 Tower nr Crater NP (17°27'S, 145°29'E); QMJ30810, Bartle Frere (17°27'S, 145°53'E); QMJ59649, Polly Ck (Hasenpusch) (17°28'S, 146°01'E); QMJ25450, Flying Fish Pt (17°3'S, 146°05'E); QMJ58921, nr Kennedy Hwy crossing of upper Barron R, 25km S of Atherton (17°32'S, 145°31'E); QMJ17435, Innisfail (17°32'S, 146°01'E); QMJ61058-59, Mt Fisher (Kjelberg Rd) (17°32'S, 145°33'E); QMJ43913, Innisfail, 25km W (17°37'S, 145°48'E); QMJ49697, Millstream NP (17°39'S, 145°27'E); QMJ34408-10, 47637, Charmillan Ck, via Ravenshoe (17°43'S, 145°31'E); QMJ48173-74, Walter Hill Ra, Charappa Ck drainage, Suttees Rd (17°43'S, 145°41'E); QMJ60892 Tully Valley, frog site (17°45'S, 145°35'E); QMJ48246-47, Forestry 'H' Rd, via Tully (17°45'S, 145°39'E); QMJ11161, 12159, Tully Falls (17°46'S, 145°34'E); QMJ48209, Billy Ck Bridge SF 758,

vicinity of bridge (17°49'S, 145°47'E); QMJ30811, Mission Beach (17°52'S, 146°06'E); QMJ51414, Kirrama Ra, BryceHenry Logging Area (18°01'S, 145°36'E); QMJ48373, Kirrama SF, Jennings Logging Area (18°04'S, 145°37'E); QMJ48369, Kirrama Ra, 2km N Kirrama Forest Stn (18°1'S, 145°43'E); QMJ48340, Kirrama Ra, Douglas Ck (18°13'S, 145°48'E); QMJ48348-49, Kirrama Ra, Kennedy Falls Logging road (18°13'S, 145°48'E); QMJ48362, Kirrama SF, Yaccabine Ck (18°13'S, 145°46'E); QMJ25022-59, 25061, Herbert Gorge (18°14'S, 145°32'E); QMJ25825-75, Cardwell (18°16'S, 146°01'E); QMJ45866, Hinchinbrook Is, Scraggy Pt (18°17'S, 146°06'E); QMJ48303, Mt MacAlister, Cardwell Ra (18°18'S, 145°56'E); QMJ48312, Cardwell Ra, Upp Broadwater Ck, Valley (18°18'S, 145°56'E); QMJ26375-76, Hinchinbrook Is, Ramsay Bay (18°19'S, 146°18'E); QMJ26330-32, Hinchinbrook Is (18°22'S, 146°15'E); QMJ44162, 44165, 44168, 44195-97, 44220, 44233, Hinchinbrook Is, Upp Gayundah Ck (18°22', 146°15'E); QMJ44169-72, 44190, 44200-13, 44216, Hinchinbrook Is, Gayundah Ck (18°22'S, 146°13'E); QMJ51409-10, Mt McAlister, 11km S (18°23'S, 145°56'E); QMJ48293, Mt Graham, 8km N Abergowrie (18°24'S, 145°52'E); QMJ51411-13, Cardwell Ra, Dalrymple Track (18°24'S, 146°04'E); QMJ45545, 45548, Mt Diamantina (18°25'S, 146°17'E); QMJ61304, Sword Ck catchment (18°27'30"S, 145°42'30"E); QMJ51415, Seaview Ra, 1st ek past Garawalt Ck Rd Xing (18°43'S, 145°44'E); QMJ49715, 49719-20, 49723, 49725-27, 49729-31 Mt Spec (18°57'S, 146°11'E); QMJ49716, Mt Spec, Little Crystal Ck (18°57'S, 146°11'E); QMJ29668, Mt Spec, Paluma (19°00'S, 146°12'E); QMJ49718, 49724, Paluma (19°00'S, 146°12'E); QMJ52995, 52997, Mt Halifax, summit ridge (19°06'S, 146°22'E); QMJ53032, Mt Halifax, 250m SE (19°06'S, 146°22'E); QMJ53039-40, Mt Halifax (19°06'S, 146°22'E); QMJ53041, Mt Halifax, 300m SE (19°06'S, 146°22'E); QMJ52996, Mt Halifax, 2.5km SE summit (19°07'S, 146°21'E); QMJ53034, Mt Halifax, 400m SE (19°07'S, 146°22'E); QMJ53035-36, Mt Halifax, 900m SE (19°07'S, 146°22'E); QMJ46774-75, Bluewater Ra, N of Townsville (19°11'S, 146°33'E); QMJ52828, 52831-33, Mt Elliot (19°28'S, 146°57'E); QMJ52830, Mt Elliot, 2km NNW of peak (19°28'S, 146°57'E); QMJ52814, 52835, 52837, Mt Elliot, 2km NW of peak (19°28'S, 146°57'E); QMJ52836, Mt Elliot, 4km NNW of peak (19°28'S, 146°57'E) QMJ59880 Cannabullen Plateau. Australian Museum. AMR56563-64, 56571, 56573 southern base of Thornton Peak (16°10'S, 145°23'E); AMR56589, 57129, Hilda Ck, southern base of Thornton Peak (16°10'S, 145°23'E); AMR59329 Thornton Peak (16°10'S, 145°23, AMR87080-81, on ridge running E-W between Thornton Peak and Daintree R (16°09'S, 145°21'E); AMR120420-22, Australian Museum- Queensland Museum rainforest survey site nr Thornton Peak (16°10'S, 145°23'E). South Australian Museum. SAMR22390, Kuranda (16°49'S, 145°38'E).

A FURTHER DIAGNOSTIC CHARACTER AND SOME BASIC BIOLOGICAL INFORMATION FOR *LERISTA COLLIVERI*. *Memoirs of the Queensland Museum* 42(2): 474, 1998.—The limb reduced, Queensland skink *Lerista colliveri* was recently recognised as distinct from *L. allanae* (Couper & Ingram, 1992; see also Shea, 1993 and Covacevich et al., 1996) on the basis of two characters, one morphological and one colour. Morphologically, *L. colliveri* differs from *L. allanae* in having the front limb represented by a nubbin versus, at most, a shallow depression. In colour pattern, *L. colliveri* differs from *L. allanae* in having continuous, dark longitudinal lines dorsally and laterally, and ventral scales with or without dark flecks versus longitudinal lines of dark spots dorsally and laterally, and ventral scales dark edged. Recent work has revealed a second morphological character distinguishing the two species, about which there had been some residual taxonomic concern (Covacevich et al., 1996), and provides an opportunity to make some general observations on *L. colliveri*, the better known of the two species. We report this new information in this note. Specimens examined in addition to those reported in Couper & Ingram, 1992 are as follows: *L. colliveri* - QMJ59904-05, 61265-66, 61270, and *L. allanae* - SAMR2823 (Shea, 1993).

The new diagnostic character for the two species of *Lerista* is the number of infralabials contacted by the postmental: one (bilaterally in 31 specimens) in *L. colliveri* vs usually two (bilaterally in 8 specimens; 1, bilaterally in 1 specimen - QMJ12232) in *L. allanae*.

The two species also differ somewhat in the way they appear to fuse supraciliaries. Both species have six as the maximum number of supraciliaries, but when there are five continuous supraciliaries (i.e., no fusions with the supraoculars), this is achieved through the fusion of supraciliaries one and two (unilaterally, AMR113538), two and three (unilaterally, AMR113526), four and five (unilaterally, AMR113516), or five and six (bilaterally, AMR113532) in *L. colliveri* (total of five cases in 25 specimens) and through the fusion of supraciliaries one and two in *L. allanae* (all five cases of supraciliary fusion in the seven specimens in which the supraciliary area is undamaged, QMJ6040, 6238, 6429-30, 12232). Thus *L. colliveri* appears to be much more variable in the way it fuses supraciliaries than does *L. allanae*.

L. colliveri has seven premaxillary teeth ($n = 25$; total), 9-12 maxillary teeth (mean = 10.2, $n = 25$; left side), and 12-15 dentary teeth (mean = 13.2, $n = 25$; left side). There is a significant positive correlation between head length (tip of snout to centre of external ear opening), and the number of maxillary teeth ($r = 0.41$, $P = 0.049$) and dentary teeth ($r = 0.72$, $P < 0.001$), and between snout-vent length and the number of maxillary teeth ($r = 0.41$, $P = 0.045$) and dentary teeth ($r = 0.66$, $P < 0.001$).

In *L. colliveri*, the least squares regression of log head length (tip of snout to centre of external ear opening) on log snout-vent length has the equation $\log \text{head length} = 0.63 \log \text{snout-vent length} - 0.29$ ($r^2 = 0.96$, $n = 15$, $P < 0.001$) for males, and $\log \text{head length} = 0.59 \log \text{snout-vent length} - 0.24$ ($r^2 = 0.97$, $n = 10$, $P < 0.001$) for females. The 95 percent confidence interval (± 0.08) for the slope of the regression for each sex (0.63 and 0.59, respectively) is well below the isometric value of 1.00, indicating that head length becomes proportionately shorter as snout-vent length increases.

The slopes of the two regression lines are not significantly different ($F = 0.55$, $df = 1, 21$, $P = 0.46$). However, the elevations are significantly different ($F = 11.22$, $df = 1, 22$, $P = 0.003$), indicating that males have relatively longer head lengths than females.

In *L. colliveri*, the least squares regression of log rear limb length on log snout-vent length has the equation $\log \text{rear limb length} = 0.57 \log \text{snout-vent length} - 0.32$ ($r^2 = 0.86$, $P < 0.001$) for males, and $\log \text{rear limb length} = 0.43 \log \text{snout-vent length} - 0.08$ ($r^2 = 0.80$, $P < 0.001$) for females. The 95 percent confidence interval (± 0.14 and ± 0.17 , respectively) for the slopes of the regression (0.57 and 0.43, respectively) for males and females fall well below the isometric value of 1.00, indicating that rear limb length becomes proportionately shorter as snout-vent length increases.

The slopes of the two regression lines are not significantly different ($F = 2.25$, $df = 1, 21$, $P = 0.15$). However, the elevations are significantly different ($F = 5.58$, $df = 1, 22$, $P = 0.03$), indicating that males have relatively longer rear limbs than females.

In *L. colliveri*, the least squares regression of log hind limb length on log head length for both sexes combined has the equation $\log \text{hind limb length} = 0.83 \log \text{head length} + 0.01$ ($r^2 = 0.84$, $P < 0.001$). The 95 percent confidence interval (± 0.15) for the slope of the regression (0.83) falls below the isometric value of 1.00, indicating that hind limb length becomes proportionately shorter as head length increases, as it does as snout-vent length increases (above). The sexes were combined because the slopes and the elevations were not significantly different between the sexes ($F = 0.87$, $df = 1, 21$, $P = 0.36$, and $F = 1.08$, $df = 1, 22$, $P = 0.31$, respectively).

Data on clutch size is available for four specimens of *L. colliveri*. Three specimens (AMR113527, 113533, 113538) collected in the vicinity of Red Falls, the Basalt Wall, N of Charters Towers (latitude: $19^{\circ}56'S$) in the period 10-12 Sept., 1984 contain a single yolk follicle in each ovary, and one specimen (QMJ33128) collected at Battery Stn (latitude: $19^{\circ}26'S$) on 12 July, 1981 contains a single shelled egg in each oviduct. These data suggest that the species is oviparous with a clutch size of two, and that egg laying may occur during the tropical dry season (QMJ33128).

Acknowledgements

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REPTILE DIVERSITY AT RISK IN THE BRIGALOW BELT, QUEENSLAND

J.A. COVACEVICH, P.J. COUPER AND K.R. McDONALD

Covacevich, J.A., Couper, P.J. & McDonald, K.R. 1998 06 29: Reptile diversity at risk in the Brigalow Belt, Queensland. *Memoirs of the Queensland Museum*. 42(2): 475-486. Brisbane. ISSN 0079-8835.

Much of the extensive Brigalow Belt (BB) of Queensland has been cleared, primarily for grazing and agriculture. As a result, the conservation status of the region's natural ecosystems is poor: 65 of 163 ecosystems of the region are classed 'endangered' or 'of concern'.

Reptile diversity and species endemism in the region are high, but many species appear to be 'at risk', presumably from clearing. One hundred and forty-eight species of reptiles occur in the BB; 13 of these are confined or virtually confined to the region; and, for a further 14 species, the BB is a significant portion of their ranges in Queensland. Type localities of 49 nominate reptile species are in the BB of Queensland. (These, vital in species delineation and attempts to maintain diversity, have been overlooked in management). At only 10 of 28 discrete type localities for reptiles in the region are there still good stands of native vegetation in which a full complement of reptile species might flourish.

Under IUCN Species Survival Commission definitions, one species (*Lerista allanae*) is critically endangered; one (*Anomalopus mackayi*) is endangered; eleven (*Rheodytes leukops*, *L. vittata*, *Diplodactylus taenicauda*, *Delma labialis*, *Paradelma orientalis*, *Anomalopus brevicollis*, *A. leuckartii*, *Denisonia maculata*, *Furina barnardi*, *F. dunmali* and *Hemiaspis damelii*) are vulnerable; one (*Acanthophis antarcticus*) is of lower risk; and four (*Delma plebeia*, *Egernia rugosa*, *Lerista cinerea*, *Menetia sadlieri*) are data deficient. Further, five species appear to be at risk on a local, BB scale: *Chlamydosaurus kingii*, *Tympanocryptis lineata*, *T. pinguicollis*, *Tiliqua rugosa* and *Aspidites ramsayi*.

The BB is an example of how a region should not be managed to maintain biodiversity. Extensive clearing of native forests, overgrazing, intensification of agriculture and proposed significant water infrastructure for further development raise serious concern about maintenance of biodiversity in this region, unless integrated nature conservation strategies are enacted urgently. □ *Brigalow Belt, reptiles, biodiversity, conservation, Queensland.*

J.A. Covacevich, P.J. Couper, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; K.R. McDonald, Department of Environment, PO Box 834, Atherton 4883, Australia; 18 November 1997.

'... Clearing of brigalow lands for crops and pasture has reaped great economic benefits but it has also had severe negative impact on native ecosystems ... flora and fauna ...' Johnson (1996).

The Brigalow Belt (the Northern and Southern Brigalow Regions) encompasses about 20% of Queensland, roughly between the 500 and 750mm isohyets, in tropical (south of Townsville) and subtropical Queensland (Fig. 1) and northern New South Wales (Stanton & Morgan, 1977; Thackway & Cresswell, 1995).

Prior to European settlement, the Brigalow Belt (BB) was a complex mosaic of woodlands (e.g., dominated by *Eucalyptus crebra* and *E. drepanophylla*; *E. populnea* and *E. brownii*; *E. melanophloia*; *E. coolabah*, *E. tereticornis* and *E. tessellaris*); forests (e.g., of *E. tereticornis* and *E. camaldulensis*); shrubby open forests (e.g., dominated by *Acacia harpophylla*, sometimes mixed with *E. cambageana*, *Cadellia pentasyeis*, *A.*

cambagei, *A. shirleyi* or *A. rhodoxylon*; diverse semideciduous vine thickets; and open grasslands (e.g., of *Dichanthium sericeum*).

The BB supports a highly diverse vegetation, classified in 163 regional ecosystems of 36 vegetation provinces (P. Sattler, pers. comm.). However, because of long European settlement (Nix, 1994) and concomitant large-scale clearing of native vegetation for grazing, farming and mining, representation of its habitat diversity, particularly on fertile soils, in conservation reserves is poor.

Some conservation reserves (national parks, conservation parks and resource reserves) have been set aside for the protection of plant/animal diversity of the region as well as spectacular scenic features like Carnarvon Gorge. These reserves range in size from less than 2ha to nearly 300,000ha and account for 2.07% of the BB, most of which is associated with rugged sandstone areas. Other native forests are partly protected in

State Forests (2,622,239ha) and Timber Reserves (140,472ha). Many BB habitats are now at risk and are of concern to land managers, wildlife/diversity managers and conservationists. The numbers of regional ecosystems classified as endangered (32) and of concern (33) (P. Sattler, pers. comm.) highlights the difficulty confronting attempts to maintain the region's biodiversity. *A. harophylla* communities, semideciduous vine thickets and native grasslands, particularly, have been extensively modified and are now extremely poorly protected in reserves, largely because they occur/occurred on the richer soils. This problem has been highlighted many times (e.g., Sattler & Webster, 1984; Gasteen, 1985, 1987; Sattler, 1986, 1993; Davie et al., 1994; and Johnson, 1996).

In a context of widespread replacement of native vegetation of the BB with crops, introduced pastures and accompanying plant and animal pests, it is not surprising that the native vertebrates, especially species restricted to the region, would be in decline. Extinct bird and mammal species once occurring solely or mainly in the BB include: *Psephotus pulcher-*

rimus, *Notomys mordax* and *Conilurus albipes*; species extinct from the BB but still extant beyond this region include *Pseudomys australis* and *Macrotis lagotis*; species whose populations have declined significantly and are now threatened include *Neochina ruficauda ruficauda*, *Erythrorhynchus radiatus*, *Lasiornis krefftii* and *Onychogalea fraenata* (Gordon, 1984; Garnett, 1992; Lee, 1995 and Maxwell et al., 1996).

Reptiles of the BB have received little attention until recently (e.g., Gordon, 1984; Covacevich et al., 1988; Czechura & Covacevich, 1985; Cogger et al., 1993; McDonald et al., 1991). Significant collections of reptile specimens from the region have been deposited in museums (notably the Queensland and Australian Museums [Brisbane, Sydney, Australia] and the California Academy

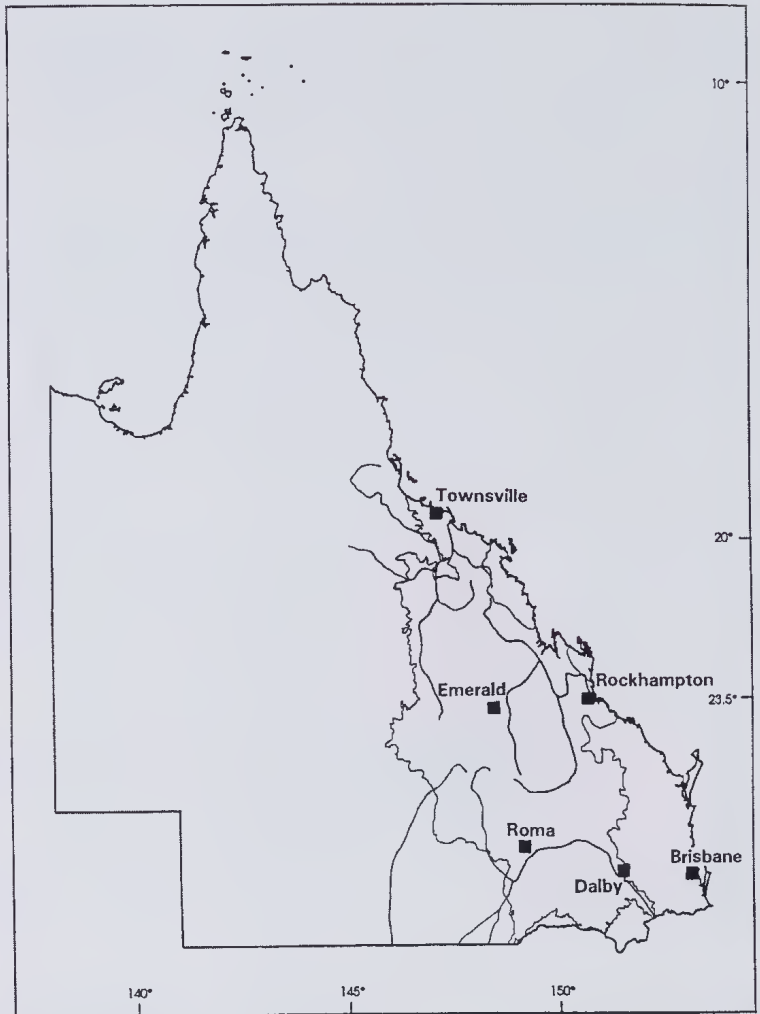


FIG. 1. Main towns/cities and river systems of Queensland's Brigalow Belt.

of Sciences in San Francisco, USA). Some general surveys of areas in the BB have included reptiles (e.g., Kirkpatrick, 1968; James, 1974; Crossman & Reimer, 1986; Russell et al., 1992; and Horsup et al., 1993) and the conservation status of some reptile species from the area has been assessed (Gordon, 1984; Covacevich et al., 1988; Czechura & Covacevich, 1985; McDonald et al., 1991; Cogger et al., 1993; Covacevich & Couper, 1996; and Covacevich et al., 1996a) but no methodical review of the distributions of all BB reptile species and their conservation status has been published.

In 1994, financial support to review museum and literature records and conduct field work to refine knowledge of the distribution and conservation status of rare or threatened BB reptile

species was received from the Australian Nature Conservation Agency (now Environment Australia). *Lerista allanae* (Longman, 1937), a species believed to be very rare, received special attention. All specimen records in the Australian Museum, the Queensland Museum and the California Academy of Sciences and all relevant records in the few BB surveys which have included reptiles were examined. Field work was undertaken in 1995 and 1996, in areas selected in an attempt to add to or clarify existing records: Emerald-Capella-Clermont district, central BB, 13-24 February, 1995 (JAC, PJC); Inglewood-Tara-Yuleba district, southern BB, 13-27 March, 1995 (JAC, PJC); Emerald-Clermont-Collinsville district, central and northern BB, 20-29 April, 1995 (JAC, PJC, KRMCD); Capella district, central BB, 9-16 February, 1996 (PJC, JAC). In all areas, standard hand-collecting, spot-lighting, and pit-trapping methods were employed. Pit-trapping has been shown to be a valuable sampling method for small species (e.g., Hannah & Smith, 1995; Hobbs et al., 1994). Voucher specimens from the field work have been added to the Queensland Museum reference collection. They bear registration numbers QMJ59368-424, QMJ59516-576, QMJ59781-870, QMJ61407-423 and QMJ61426-461.

Major findings (published) of this study are: maintenance of reptile diversity in the BB appears to be unlikely in the face of further clearing of native vegetation (Covacevich, 1996); *Lerista allanae* is at least critically endangered and may be extinct (Covacevich et al., 1996a); *Aspidites ramseyi* (Macleay, 1882) is vulnerable in the southern portion of the BB (Covacevich & Couper, 1996); and, despite extensive clearing in the Emerald district, a highly diverse array of small reptiles survives in a disturbed *Callitris* forest close to Emerald (Deer, 1996). Further, incidental observations made during the study have enhanced knowledge of *Nephurus asper*, *Gehyra dubia* and *Vermicella annulata* (Couper, 1996; Couper et al., 1995; and Couper et al., 1996) and of the previously unknown donor of the holotype of *Lerista allanae*, Maida Allan (Covacevich & Couper, 1997).

REPTILE DIVERSITY OF QUEENSLAND'S BRIGALOW BELT

One hundred and forty-eight species of reptiles are known from Queensland's BB (Appendix 1). The occurrence of these species has been mapped from collection/sight localities which have been listed in an unpublished report lodged with Environment Australia (Canberra) and in the Library,

Queensland Museum (Brisbane), accession number 97/22378, Covacevich et al., 1996b.

The ranges of 13 species are confined to, or virtually confined to the BB: *Rheodytes leukops* Legler & Cann, 1980; *Diplodactylus taenicauda* De Vis, 1886 (Fig. 2); *Paradelma orientalis* (Günther, 1876); *Anomalopus brevicollis* Greer & Cogger, 1985; *Anomalopus mackayi* Greer & Cogger, 1985; *Ctenotus ingrami* Czechura & Wombey, 1982; *Lampropholis mirabilis* Ingram & Rawlinson, 1981; *Lerista allanae* (Longman, 1937); *Lerista vittata* Greer, McDonald & Lawrie, 1983; *Menetia sadlieri* Greer, 1991; *Denisonia maculata* (Steindachner, 1867); *Furina dunmali* (Worrell, 1955); *Hemiaspis damelii* (Günther, 1876). For a further 14 species, the BB is a significant part of their ranges in Queensland: *Chelodina expansa* Gray, 1867; *Gehyra catenata* Low, 1979; *Oedura monilis* De Vis, 1888; *Saltuarius salebrosus* (Covacevich, 1975); *Anomalopus leuckartii* (Weinland, 1862); *Egernia modesta* Storr, 1968; *E. rugosa* De Vis, 1888; *Eulaniprus sokosoma* Greer, 1992; *Glaphyromorphus punctulatus* (Peters, 1871); *Lerista fragilis* (Günther, 1876); *Menetia timlowi* Ingram, 1977; *Hoplocephalus bitorquatus* (Jan, 1859); *Pseudechis guttatus* De Vis, 1905; and *Suta dwyeri* (Worrell, 1956) = *S. spectabilis dwyeri* (Worrell, 1956).

CONSERVATION STATUS

Given that much of the BB has been cleared, that 40% of its regional ecosystems are classed endangered or of concern, that several bird and mammal species formerly from the area are extinct and that populations of many bird and mammal species of the region have declined seriously, it is predictable that reptile species of the BB would be at risk. Species confined to or occurring predominantly in the region are of most concern. Prior to this study, three authorities had afforded special conservation status to reptile species from the BB in Queensland (McDonald et al., 1991; Cogger et al., 1993; Queensland Nature Conservation (Wildlife) Regulation 1994). Table 1 summarises the status of rare and threatened species of reptiles of this region according to these authors.

In November, 1994, the 40th meeting of the IUCN Council of the IUCN Species Survival Commission prepared '... new definitions for Red List categories ...' of threatened species. In the light of these, following our field work and review of reptile specimen records in museums and relevant literature, the current conservation status of



FIG. 2. One of 15 reptile species currently at risk in Queensland's Brigalow Belt. *Diplodactylus taeniocauda* is vulnerable. Specimen collected (and released) near Yulcba, SCQ, 21 March, 1995, during extensive reptile surveys in the region. (J. Wright, Queensland Museum)

species of special concern at the national/international level can be assessed. Under the IUCN (1994) definitions one species is critically endangered; one is endangered; 10 are vulnerable; two are at lower risk, near threatened; and four are data deficient (Table 2).

Under the IUCN definitions, one BB reptile species previously classed rare or threatened (McDonald et al., 1991; Cogger et al., 1993; Nature Conservation (Wildlife) Regulation, 1994) does not qualify for special conservation status. *Chelodina expansa* of rivers and lagoons in and beyond the BB is apparently not presently at risk. Another species (*Lampropholis mirabilis*), formerly classed rare and threatened (McDonald et al., 1991; Cogger et al., 1993; Nature Conservation (Wildlife) Regulation, 1994) warrants discussion. *L. mirabilis* clearly is a vulnerable (VU D2) species: '... population very small or restricted ... acute restriction in its area of occupancy ... thus prone to the effects of human

activities (or stochastic events) ...'. This species is known from only three localities (Magnetic I., Cape Cleveland and Mt Elliot, all near Townsville, NEQ, in the north-east part of the BB over an area considerably smaller than 100km². The full known range of this species is secure in national parks. Thus, given that this species is not prone to any identifiable threats, we do not regard it as being vulnerable.

A further 5 reptile species appear to be at risk in the BB: *Chlamydosaurus kingii* Gray, 1825 is primarily a species of northern and coastal Queensland. Two museum specimens (QMJ15592 - 97km E of Clermont, 22°48'S 148°31'E; QMJ33566 - Coorara stockroute, ca 55km ENE of Emerald, 23°05'S 148°25'E) attest to the occurrence of this species in the BB. These were registered in 1968 and 1990 respectively. Reliable, more recent sight records have been made in the BB: 20 Feb., 1992, Epping Forest 22°19'S 146°45'E, (G. Porter, Department of Environment, pers. comm.); 13 Feb., 1995 Taunton, 23°30'S 149°15'E (G. Porter, pers. comm.); Feb. and Oct., 1991 Wonga Hills, 26°06'S 150°45'E (Russell et al., 1992). *C. kingii* is a species well-known and frequently-reported elsewhere. Records of this species in the BB appear both to be and to have been scant, and most of the few localities from which it is known have been modified for farming or grazing. Epping Forest and Taunton, where specimens of *C. kingii* were seen in 1992 and 1995, are small national parks. This affords some hope for the survival of this species in the BB.

Tympanocryptis lineata Peters, 1863 was classed by Gordon (1984) in the first review of fauna (=mammals, primarily) of the BB as 'a lizard of the blue grass downs of central Queensland'. 'Natural grasslands, downs...' he noted '... were greatly favoured by early settlers and have been subject to heavy grazing since first settlement...'. Since these surveys of the 1970s and the Gordon (1984) review, much of the area near Emerald where *T. lineata* occurred has been developed for agriculture. Museum specimens of *T. lineata* have not been collected recently: 2 April, 1976, Emerald Downs 23°29'S 148°08'E (QMJ36851); 4 Jan., 1976, Selma 23°31'S 148°02'E (QMJ36849); 5 Oct., 1976, 22 Sept., 1976, 5 Oct., 1976, Iona 23°32'S 147°57'E (QMJ36853, QMJ36848, QMJ36852); Nov., 1977, nr Emerald 23°32'S 148°15'E (QMJ36847); 10, 19, 22 Aug., 1929, 9 Sept., 1929 Retro 20m W of Capella 22°52'S 147°54'E (Cal. Acad. 77623-77626).

TABLE 1. Rare and threatened species of reptiles from Queensland's BB according to three recent authorities.

Species	Authority		
	McDonald et al., 1991	Cogger et al., 1993	Nature Conserv- ation (Wildlife) Regulation 1994
<i>Chelodina expansa</i>	—	rare or insufficiently known	—
<i>Emydura macquarii</i>	—	rare or insufficiently known	—
<i>Rheodytes leukops</i>	very restricted, poorly known	vulnerable	vulnerable
<i>Diplodactylus taenicauda</i>	—	rare or insufficiently known	rare
<i>Delma labialis</i>	very restricted, rare	vulnerable	vulnerable
<i>Paradelma orientalis</i>	restricted to specific habitats, vulnerable	vulnerable	vulnerable
<i>Anomalopus brevicollis</i>	restricted to specific habitats, poorly known, occurring in reserves	—	rare
<i>Anomalopus mackayi</i>	restricted to specific habitats, poorly known	vulnerable	vulnerable
<i>Ctenotus eutaenius</i>	restricted to specific habitats, poorly known, occurring in reserves	—	—
<i>Egernia rugosa</i>	restricted to specific habitats, rare	rare or insufficiently known	vulnerable
<i>Lampropholis mirabilis</i>	very restricted, rare, occurring in reserves	rare or insufficiently known	rare
<i>Lerista allanae</i>	restricted to specific habitats, rare	endangered	endangered
<i>Lerista cinerea</i>	very restricted, poorly known	rare or insufficiently known	rare
<i>Lerista vittata</i>	very restricted, poorly known	vulnerable	vulnerable
<i>Menetia sadleri</i>	—	rare or insufficiently known	rare
<i>Acanthophis antarcticus</i>	—	rare or insufficiently known	rare
<i>Denisonia maculata</i>	restricted to specific habitats, vulnerable, occurring in reserves	vulnerable	vulnerable
<i>Furina barnardi</i>	—	rare or insufficiently known	rare
<i>Furina dunmalli</i>	restricted to specific habitats, vulnerable, occurring in reserves	vulnerable	vulnerable

T. pinguiicola Mitchell, 1948 was described as a subspecies of *T. lineata*. Concern about prospects for survival of '*T. lineata pinguiicola*' has been expressed recently because of 'substantial loss and modification of native grasslands in south-eastern Australia' (Osborne et al., 1993). Current taxonomic review of *Tympanocryptis* spp. indicates that *T. pinguiicola* is a distinct species (A. Greer, pers. comm., Nov., 1997). In southern Queensland, *T. pinguiicola* appears to have an extremely restricted range. It has been recorded only near the southeastern boundary of the BB, in the Oakey district. Museum holdings of this species are scant and not recent: no date, Bougeen near Oakey 27°34'S 151°27'E (QMJ8604); Dec., 1978, 30km S of Oakey 27°39'S 151°36'E (QMJ34744). There have been no recent reports of sightings of *T. pinguiicola* in the southern BB, despite considerable field work in and near appropriate localities. The case of *T. pinguiicola* at the north-eastern limit of its range in the BB of Queensland parallels a major conservation problem highlighted by Daugherty et al., 1990 for *Sphenodon* spp. In reviewing the conservation/management of these species, they showed how a lack of awareness of species/'taxonomic neglect' could lead to extinction.

Tiliqua rugosa (Gray, 1825) is a large, conspicuous skink. Many museum specimens of this species, frequently obtained as 'road-kills', are held from the BB (e.g., Ingram & Raven, 1991). This is an easily-identified species reported often. In Queensland it has been recorded subtropically and subcoastally in the BB and mulga lands immediately to the west of the BB. The last BB specimen added to the Queensland Museum collections is QMJ58785 (Mungallala 26°27'S 147°33'E, Dec., 1993). No specimens were seen during our field work in the BB. This included intensive work on Retro Station and the lands which were formerly part of this station, a known former locality of *T. rugosa* (Cal. Acad. 76652-76653, 8, 14 August, 1929). Retro has been cleared almost entirely of native vegetation. Whether *T. rugosa* populations have declined in recent years has not been shown conclusively. However, probable local declines have been suggested also by other herpetologists who have worked in the BB (S. Irwin and C. Eddie, pers. comms).

Aspidites ramsayi (Macleay, 1882) has recently been shown to be vulnerable in the southern BB (Covacevich & Couper, 1996).

TABLE 2. Conservation status of reptile species at risk in the BB of Queensland, under IUCN Species Survival Commission definitions of 1994.

Species	Conservation Status		
<i>Lerista allanae</i>	'critically endangered'	'(CE) C2a'	'Population estimated to number less than 250 individuals ... A continuing decline...'
<i>Anomalopus mackayi</i>	'endangered'	'(EN) A1c'	'Population reduction ... of over 50% over the last 10 years ... based on ... decline in quality of habitat...'
<i>Rheodytes leukops</i> <i>Lerista vittata</i>	'vulnerable'	'(VU) D2'	'Population restricted ... characterised ... by an acute restriction in its area (typically less than 100km ²) ... the number of locations (typically less than 5)...'
<i>Paradelma orientalis</i> <i>Diplodactylus taenicauda</i> <i>Anomalopus brevicollis</i> <i>Anomalopus leuckartii</i> <i>Denisonia maculata</i> <i>Furina barnardi</i> <i>Furina dunmalli</i> <i>Hemiaspis damelii</i>	'vulnerable'	'(VU) A1c'	'Population reduction ... decline in area of extent of occurrence and ... quality of habitat ...'
<i>Acanthophis antarcticus</i> <i>Delma labialis</i>	'lower risk, near threatened'	'(LR) 2nt'	'... close to qualifying for vulnerable ...'
<i>Delma plebeia</i> <i>Egernia rugosa</i> <i>Lerista cinerea</i> <i>Menetia sadleri</i>	'data deficient'		'inadequate information ... appropriate data on abundance and/or distribution is lacking ... possibility that future research will show ... threatened ... is appropriate'

Our field work and a study arising from it (Deer, 1996) have shown that reptile diversity can remain high in protected reserves and state lands of the BB (e.g., Dipperu N.P./16 species; Yuleba SF/25 species); reptile diversity can remain high in the face of considerable disturbance of a forest (e.g., Fairbairn Dam remnant *Callitris* forest with 24 small reptile species); and predictably, that agricultural lands are depauperate in terms of reptile diversity. Although *Pogona barbata* (Cuvier, 1829), *Tiliqua scincoides* (White ex Shaw, 1790), *Antaresia maculosus* (Peters, 1873) and *Pseudonaja textilis* (Duméril, Bibron & Duméril, 1854) to remain conspicuous (?common) on and near roads in agricultural areas and fringing strips of forest and weeds, agricultural lands apparently support fewer species than reported previously from these areas prior to clearing (e.g., Slevin, 1955; Covacevich et al., 1996b).

DISCUSSION

Biodiversity has declined in the BB due to clearing of native vegetation. Only 2.07% of the region is set aside expressly for protection of biodiversity; a further 4% is afforded some protection in state lands. Forty percent of the regional ecosystems are known to be at risk, with most Brigalow systems endangered. One reptile species is critically endangered, possibly extinct; 16 are at risk; and 5 are of concern locally. There will be additions to the list of critically endangered-vulnerable species (13) and more species will be recognised as being at risk if the threatening processes responsible for past demises are not modified.

In return for clearing much of the BB there have been many gains.

'... Originally a sheep raising district, the fertile soils now support extensive grain-growing, chiefly wheat but including barley, maize, oats and oilseeds; irrigated land in the west produces cotton. Dairy and beef cattle are also important, and oil, natural gas and coal are natural resources ...' (Dawson, 1990). '... In 1982, (Emerald's) population was about 4,500. Today, Emerald is a boom town. Its wealth is derived from cattle, cotton, oranges, wheat, sorghum, mung beans, sunflower seeds, and coal and gold mines. In the principal catchment area of Emerald, there are now 50,000 people, most of whom must be living well, because the average annual household income in the area is \$45,000 ...' (Hay, 1995). Large financial investments are proposed to continue to increase productivity. This will involve further clearing and intensification of land use. In 1995, the Queensland Government '... endorsed a plan to investigate three water infrastructure development projects in the Fitzroy Basin ... pipeline from Eungella Dam to the central Queensland coalfields(; a proposed dam on the Dawson River to provide urban, industrial and irrigation water ... to existing and new land ... to be developed (; and) ... a proposed dam on the Comet River to provide urban, industrial and irrigation supplies to lands adjacent to the Comet, Nogoa and MacKenzie Rivers ...' (Queensland Department of Primary Industries, undated, ?1995). A recent report of the Queensland Government's

Water Infrastructure Task Force (1997) recommends for the BB, eight Category 1 water supply projects suitable for continuation or commencement of detailed planning and assessment; three for regional planning and assessment studies; two for groundwater projects; and one general proposal for water supply research, catchment management and on-farm water conservation. The Task Force also recognised 'All infrastructure development projects should be subject to satisfactory outcomes of normal impact assessment studies (including environmental, economic, social and cultural impacts) and negotiation of satisfactory funding arrangements prior to recommendation for funding by Government ...'. Further, all Australian state governments have recently (July, 1996) signed 'National Principles for the Provision of Water for Ecosystems' following representations to the Australian and New Zealand Environment and Conservation Council and the Agriculture and Resource Management Council of Australia and New Zealand. A major goal of these principles is '... providing water for the environment ... to sustain and, where necessary, restore ecological processes and biodiversity of water dependent systems ...'. The construction of dams will lead to increased pressures on the reptiles (and other species) of the BB, through progressive intensification and expansion of agriculture and associated infrastructure. This impact will not only occur in areas directly affected, ie the irrigation areas. The size of this investment will encourage development across the whole region. This, in turn, will threaten remaining significant remnants of native vegetation. By comparison, proposals to address nature conservation in the BB have not yet been accepted as urgent.

IMPORTANCE OF TYPE LOCALITIES. In any area as assailed by clearing as is the BB, type localities, critical in species delineation, become important in the preservation of diversity. This principle applies particularly where species are narrowly confined or virtually-confined to a region as are many of the reptile species of the BB. The type locality is '... the place where the population occurs from which the type specimen [i.e., the specimen on which the description and name of any species are based] was taken ... The "type" affords the standard of reference that determines the application of the scientific name ...': [] ours (Rules of Zoological Nomenclature in Mayr, 1969).

Some BB type localities for reptile species have been published (Covacevich, 1996). The

complete list of BB type localities for reptile species is extensive (Table 3). Many were poorly-defined in early type descriptions; many are now cities or towns; and some have been cleared for agriculture and/or grazing. Only a few support anything like the vegetation present when the type specimens were collected. Those where good tracts of native (and near native) vegetation remain are highlighted in Table 3.

LESSONS FROM THE BRIGALOW BELT. The BB in Queensland is a fine example of how to diminish diversity — encourage clearing of native forests, through taxation and other incentives; fail to secure in conservation reserves representatives of all vegetation types in the region; recognise late, after several species have become extinct or are in decline, that a major problem in maintaining diversity exists; and proceed with plans for further development even though diversity is already known to be assailed. As attempts progress to improve biodiversity protection in the BB, lessons from other settings become relevant:

1) Research/management attention focussed narrowly on a particular habitat/region or on rare species is, inevitably, costly for other habitats/regions/species (e.g., Voous, 1977; Covacevich & McDonald, 1993).

2) 'We should pay more attention to habitats rather than concentrating heavily or solely on special-interest taxa' (Czechura & Covacevich, 1985).

3) Although habitat protection is the best approach to species protection, it cannot guarantee species survival and habitat destruction guarantees loss of species (e.g., Ingram & McDonald, 1993; Covacevich et al., 1996).

4) '... fauna protection authorities ... have tended to approach reptile conservation by ... restrictions on ... collecting and keeping ... (so) much emphasis has been placed on rare and endangered species, a flawed approach, which allows statutory protection of habitat and mandatory requirements that wildlife authorities monitor populations ...' (Rawlinson, 1981, in Czechura & Covacevich, 1985).

5) Perhaps most important is the finding that '... Species-rich areas ('hot spots') frequently do not coincide for different taxa, and many rare species do not occur in the most species-rich (areas) ...' (Prendergast et al., 1993).

In the Queensland BB it is apparent that small, remnant patches of native vegetation support many reptile species. However, a paucity of data makes it impossible to determine whether or not these areas can sustain reptile populations in the

TABLE 3. Queensland BB type localities for nominate reptile species. Type localities where good tracts of native vegetation remain are highlighted *.

Warrawee Stn, 60km SE 20°24' 146°40'*	<i>Lerista cinerea</i> Greer, McDonald & Lawrie, 1983	restricted to Rockhampton	<i>Hoplocephalus maculatus</i> Steindachner, 1867 = <i>Denisonia maculata</i> (Steindachner, 1867)
Mt Cooper Stn, 90km SE 20°31'S 146°47'E	<i>Lerista vittata</i> Greer, McDonald & Lawrie, 1983	Rockhampton and Peak Downs	<i>Hoplocephalus damelii</i> Günther, 1876 = <i>Hemiaspis damelii</i> (Günther, 1876)
Bowen (as Port Denison)	<i>Aspidotes melancephalus</i> Krefft, 1864 = <i>Aspidites melanocephalus</i> (Krefft, 1864)	Rockhampton, 1km E of Frenchville 23°22'S 150°32'E	<i>Anomalopus brevicollis</i> Greer & Cogger, 1985
Bulliwallah Stn, on Belyando R., via Clermont *	<i>Varanus bulliwallah</i> Worrell, 1956 = <i>Varanus mertensi</i> Glauert, 1951	Fitzroy R., 63km N & 22km E of Duaringa, elevation 40m, 23°09'S 149°55'E	<i>Rheodytes leukops</i> Legler & Cann, 1980
Barmount 80km NW Marlborough 22°32' 149°06' MEQ*	<i>Menetia timlowi</i> Ingram, 1977	19km W of Emerald 81.5km E of Bogantungan*	<i>Oedura attenboroughi</i> Wells & Wellington, 1985
Batheaston Stn 22°26'S 148°47'E*	<i>Gehyra catenata</i> Low, 1979	15 miles S Duaringa	<i>Glyphodon barnardi</i> Kinghorn, 1939 = <i>Furina barnardi</i> (Kinghorn, 1939)
Lake Elphinstone	<i>Tropidolepisma striolatum</i> Peters, 1870 = <i>Egernia striolata</i> (Peters, 1870) <i>Hoplocephalus frenatus</i> Peters, 1870 = <i>Suta suta</i> (Peters, 1863)	State Forest, foothills of Mt Larcom 23°49'S 151°22'E*	<i>Heteropus mundus</i> De Vis, 1885 = <i>Carlia munda</i> (De Vis, 1885)
Retro, Capella	<i>Rhodona allanae</i> Longman, 1937 = <i>Lerista allanae</i> (Longman, 1937)	Gyandra, Dawson R. (as Upper Dawson R.)	<i>Lygosoma bancrofti</i> Longman, 1916 = <i>Anomalopus leuckartii</i> (Weinland, 1862)
Peak Downs	<i>Diplodactylus steindachneri</i> Boulenger, 1885 <i>Nephrurus asper</i> Günther, 1876 <i>Delma orientalis</i> Günther, 1876 = <i>Paradelma orientalis</i> (Günther, 1876) <i>Rhodona fragilis</i> Günther, 1876 = <i>Lerista fragilis</i> (Günther, 1876) <i>Lygosoma heterodactylum</i> Günther, 1876 = <i>Glaphyromorphus punctulatus</i> (Peters, 1871)	Port Curtis*	<i>Simotes australis</i> Krefft, 1864 = <i>Smoselaps australis</i> (Krefft, 1864)
Central Queensland	<i>Grammatophora inermis</i> De Vis, 1888 = <i>Ctenophorus nuchalis</i> (De Vis, 1884)	Monto	<i>Phyllurus salebrosus</i> Covacevich, 1975 = <i>Saturius salebrosus</i> (Covacevich, 1975)
neighbourhood of Rockhampton	<i>Hoplocephalus nigrostriatus</i> Krefft, 1864 = <i>Rhinoplocephalus nigrostriatus</i> (Krefft, 1864) <i>Hoplocephalus nigrostriatus</i> Krefft, 1864 = <i>Rhinoplocephalus nigrostriatus</i> (Krefft, 1864)	Eidsvold, Upper Burnett R.*	<i>Varanus punctatus orientalis</i> Fry, 1913 = <i>Varanus tristis</i> (Schlegel, 1839)
near Rockhampton	<i>Denisonia ornata</i> Krefft, 1869 = <i>Denisonia maculata</i> (Steindachner, 1867)	Burnett River *	<i>Diemenia maculiceps</i> Boettger, 1898 = <i>Demansia vestigiata</i> (De Vis, 1884) <i>Lygosoma verreauxii biunguiculata</i> Oudemans, 1894 = <i>Anomalopus leuckartii</i> (Weinland, 1862)
Rockhampton	<i>Heteropus schmeltzii</i> Peters, 1867 = <i>Carlia schmeltzii</i> (Peters, 1867) <i>Pseudechis scutellatus</i> Peters, 1867 = <i>Oxyuramus scutellatus</i> (Peters, 1867) <i>Himulia fasciolata</i> Günther, 1867 = <i>Eremiascincus fasciolatus</i> (Günther, 1867) <i>Tiliqua longicauda</i> De Vis, 1888 = <i>Cyclodomorphus gerrardii</i> (Gray, 1845) (designated by Wells & Wellington, 1985) <i>Phyllodactylus anomalus</i> Peters, 1867 = <i>Heteronotia binocci</i> (Peters, 1867) <i>Pseudechis scutellatus</i> Peters, 1867 = <i>Oxyuramus scutellatus</i> (Peters, 1867) <i>Typhlops (Onychchocephalus) unguirostris</i> part Peters, 1867 = <i>Ramphotyphlops unguirostris</i> (Peters, 1867)	Chinchilla	<i>Diplodactylus taenicauda</i> De Vis, 1886 <i>Egernia whitei modesta</i> Storr, 1968 = <i>Egernia modesta</i> (Storr, 1968)
		Chinchilla, Darling Downs	<i>Heteropus vertebralis</i> De Vis, 1888 = <i>Carlia mundivensis</i> (Broom, 1898)
		Mowen (?=Morven) central railway	<i>Typhlops diversus</i> Waite, 1894 = <i>Ramphotyphlops diversus</i> (Waite, 1894)
		Glenmorgan*	<i>Glyphodon dummalli</i> Worrell, 1955 = <i>Furina dummalli</i> (Worrell, 1955) <i>Denisonia dwyeri</i> Worrell, 1956 = <i>Suta dwyeri</i> (Worrell, 1956)
		near Surat	<i>Hoplocephalus ornatus</i> De Vis, 1884 = <i>Denisonia devisi</i> (Waite & Longman, 1920)
		Cecil Plains, SEQ	<i>Pseudechis guttata</i> De Vis, 1905
		Moombah Stn., ca 64km W Westmar, ca 60km NE St George, SEQ 27°59'S 149°18'E*	<i>Ctenopus ingrami</i> Czechura & Wombey, 1982

long term. Our recent field work in the BB has shown that reptile diversity in some areas, all still supporting native vegetation, is high. However, despite the intensity of this work and success in finding reptiles, few of the 20 species at risk in

the BB were encountered. In Dipperu NP, none of these species was found; in Inglewood SF one (*Acanthophis antarcticus*) was found and one (*Paradelma orientalis*) has been found since (Schultz & Eyre, 1997); in *Callitris* forest near

Emerald, one (*Diplodactylus taenicauda*) was common (Deer, 1996); and an isolated population of *Aspidites ramsayi* is well-known in the Yuleba district. These results superficially support the findings of Prendergast et al., 1993, that '... A limited number of species-rich areas do not guarantee effective conservation for rare and restricted organisms, many of which occur outside species-rich areas ...'. However, they are far from a thorough assessment of the question of the coincidence of diversity hotspots and rare species in the BB.

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APPENDIX 1

Reptile species of the Brigalow 'Belt' of Queensland.

Family Chelidae

- Chelodina expansa* Gray, 1857
C. longicollis (Shaw, 1802)
Elseya dentata (Gray, 1863)
E. irwini Cann, 1997
E. latisternum Gray, 1867
E. mydura krefftii (Gray, 1871)
E. macquarii (Gray, 1831)
Rheodytes leukops Legler & Cann, 1980

Family Gekkonidae

- Diplodactylus conspicillatus* Lucas & Frost, 1897
D. steindachneri Boulenger, 1885
D. taenicauda De Vis, 1886
D. tessellatus (Günther, 1875)
D. vittatus Gray, 1832
D. williamsi Kluge, 1963
Gehyra catenata Low, 1979
G. dubia (Macleay, 1877)
G. variegata (Duméril, 1836)
Heteronotia binoei Gray, 1845
Nephurus asper Günther, 1876
N. milii (Bory de St Vincent, 1825)
Oedura castelnaui Thominot, 1889
O. lesueurii (Duméril & Bibron, 1836)
O. marmorata Gray, 1842
O. monilis De Vis, 1888
O. rhombifer Gray, 1845
O. robusta Boulenger, 1885
O. tryoni De Vis, 1885
Rhynchoedura ornata Günther, 1867
Saltuarius salebrosus (Covacevich, 1975)

Family Pygopodidae

- Delma inornata* Kluge, 1974
D. labialis Shea, 1987
D. plebeia De Vis, 1888
D. tinctoria De Vis, 1888

- Lialis burtonis* Gray, 1835
Paradelma orientalis (Günther, 1876)
Pygopus nigriceps Fischer, 1882

Family Scincidae

- Anomalopus brevicollis* Greer & Cogger, 1985
A. leuckartii (Weinland, 1862)
A. mackayi Greer & Cogger, 1985
A. verreauxii Duméril, 1851
Carlia jarnoldae Covacevich & Ingram, 1975
C. munda (De Vis, 1885)
C. mundivensis (Broom, 1898)
C. pectoralis (De Vis, 1885)
C. schmetzii (Peters, 1867)
C. tetradactyla (O'Shaughnessy, 1879)
C. vivax (De Vis, 1885)
Cryptoblepharus carnabyi (Storr, 1976)
C. plagiocephalus (Cocteau, 1836)
C. virgatus (Garman, 1901)
Ctenopus allotropis Storr, 1981
C. eutaenius Storr, 1981
C. hebetior Storr, 1978
C. ingrami Czechura & Wombey, 1982
C. pantherinus Peters, 1866
C. robustus Storr, 1971
C. strachii (Boulenger, 1887)
C. taeniolatus (Shaw, 1790)
Cyclodomorphus gerrardii (Gray, 1845)
Egernia cunninghami (Gray, 1832)
E. frerei Günther, 1897
E. modesta Storr, 1968
E. rugosa De Vis, 1888
E. striolata Peters, 1870
Eremiascincus fasciolatus (Günther, 1867)
E. richardsoni (Gray, 1845)
Eulanprus brachysoma (Lönnberg & Andersson, 1915)
E. martini Wells & Wellington, 1985
E. quoyii (Duméril & Bibron, 1839)
E. sokosoma Greer, 1992
E. tenuis Gray, 1831
Glaphyromorphus punctulatus (Peters, 1871)
Lampropholis delicata (De Vis, 1888)
L. mirabilis Ingram and Rawlinson, 1981
Lerista allanae (Longman, 1937)
L. cinerea Greer & McDonald & Lawrie, 1983
L. fragilis (Günther, 1876)
L. muelleri (Fischer, 1881)
L. punctatovittata (Günther, 1867)
L. vittata Greer, McDonald & Lawrie, 1983
Lygisaurus foliorum De Vis, 1884
Menetia greyii Gray, 1845
M. sadlieri Greer, 1991
M. timlowi Ingram, 1977
Morethia boulengeri (Ogilby, 1890)
M. taeniopleura (Peters, 1874)
Proablepharus kinghorni (Copland, 1947)
Saiphos equalis (Gray, 1825)
Tiliqua multifasciata Sternfeld, 1919
T. rugosa (Gray, 1827)
T. scincoides (Shaw, 1790)

Family Agamidae

- Amphibolurus burnsi* (Wells & Wellington, 1985)

- A. gilberti* (Gray, 1842)
A. muricata (Shaw, 1790)
A. nobbi Witten, 1972
Chlamydosaurus kingii Gray, 1825
Ctenophorus nuchalis (De Vis, 1885)
Diporiphora australis (Steindachner, 1867)
Physignathus lesueurii (Gray, 1831)
Pogona barbata (Cuvier, 1829)
Tympanocryptis lineata Peters, 1863
T. pingüicollis Mitchell, 1948

Family Varanidae

- Varanus gouldii* (Gray, 1838)
V. mertensi Glauert, 1951
V. panoptes Storr, 1980
V. scalaris Mertens, 1941
V. tristis (Schlegel, 1839)
V. varius (Shaw, 1790)

Family Typhlopidae

- Ramphotyphlops affinis* (Boulenger, 1889)
R. bituberculatus (Peters, 1863)
R. grypus (Waite, 1918)
R. ligatus (Peters, 1879)
R. proximus (Waite, 1893)
R. unguirostris (Peters, 1867)
R. wiedii (Peters, 1867)

Family Boidae

- Antaresia maculosa* (Peters, 1873)
Aspidites melanocephalus (Krefft, 1864)
A. ramsayi (Macleay, 1882)
Morelia spilota (Lacépède, 1804)

Family Colubridae

- Boiga irregularis* (Merren, 1802)
Dendrelaphis punctulata (Gray, 1827)
Tropidonophis mairii (Gray, 1841)

Family Elapidae

- Acanthophis antarcticus* (Shaw, 1794)
Cacophis harriettae Krefft, 1896
Demansia papuensis (Macleay, 1877)
D. psammophis (Schlegel, 1837)
D. torquata (Günther, 1862)
D. vestigiata (De Vis, 1884)
Denisonia devisi Waite & Longman, 1920
D. maculata Steindachner, 1867
Furina barnardi (Kinghorn, 1939)
F. diadema (Schlegel, 1837)
F. dunmalli (Worrell, 1955)
Hemiaspis damelii (Günther, 1876)
Hoplocephalus bitorquatus (Jan, 1859)
Notechis scutatus (Peters, 1861)
Pseudechis australis (Gray, 1842)
P. guttatus De Vis, 1905
P. porphyriacus (Shaw, 1794)
Pseudonaja nuchalis Günther, 1858
P. textilis (Dumeril, Bibron, & Dumeril, 1854)
Rhinoplocephalus boschmai (Brongersma & Knaap-van Meeuwen, 1961)
R. nigrescens (Günther, 1862)
R. nigrostriatus (Krefft, 1864)
Simoselaps australis Krefft, 1864
Suta dwyeri (Worrell, 1956)
S. suta (Peters, 1863)
Vermicella annulata (Gray, 1841)

TWO NEW SEMI-AQUATIC SPECIES OF *DIPLOTREMA* (OLIGOCHAETA: MEGASCOLECIDAE: ACANTHODRILINAE), WITH A RE-DESCRIPTION OF THE TYPE SPECIES

G. R. DYNE AND B.G.M. JAMIESON

Dyne, G.R. & Jamieson, B.G.M. 1998 06 29: Two new semi-aquatic species of *Diplo-*
trema (Oligochaeta: Megascolecidae: Acanthodrilinae), with a re-description of the type species.
Memoirs of the Queensland Museum 42(2): 487-493. Brisbane. ISSN 0079-8835.

Two new species of the genus *Diplo-*
trema sharing a suite of morphological characters and
a semi-aquatic mode of life are described. Together with the previously described *D.*
tyagarah, they are placed in a species-group the nominate species of which is the generic
type-species, *D. fragilis*. The latter taxon, of pivotal importance in early phylogenetic
schemes owing to an erroneous determination of the condition of the male pores, is
redescribed from the syntypes. □ *Earthworms, Megascolecidae, Diplo-*
trema, semi-aquatic.

G.R. Dyne, *Environment Australia, PO Box 787, Canberra ACT 2600, Australia*; B.G.M.
Jamieson, *Department of Zoology, University of Queensland, St Lucia 4072, Australia*; 4
May 1997.

The significance of the type-species of *Diplo-*
trema, *D. fragilis* Spencer, in the inferred phylo-
geny of the Megascolecidae proposed by
Stephenson (1930) has been outlined by Jamieson
(1971) and Dyne (1978). More recent studies
(Jamieson & Dyne, 1976; Dyne, 1984) have
shown that the genus is far more widespread and
speciose than previously believed, and that dis-
tinct species-groups are recognisable.

The two new species described here confirm the
concept of a species-group including the type-
species of the genus and a number of morphologi-
cally similar species inhabiting a similar ecotype.
The collection of these species at sites either
subject to periodic inundation, or permanently
below the water-table, testifies to their semi-
aquatic propensities. This represents exploitation
of a niche largely unfilled by other Australian
megascolecids. Some *Spenceriella* species are known
from swampy habitats, however (Dyne, 1984).

SYSTEMATICS

Members of the *Diplo-*
trema fragilis species-
group share the following character set: pros-
tomium epilobous, nephropores in the vicinity of
cd, slender body form, ♂ pores slightly presetal,
intersegmental markings restricted to the region
of segments XVI-XX, genital seta follicles
strongly developed in VII, VIII or IX, often with
associated glands, penial setae fine and delicate
with little or no ornamentation, pharyngeal tufted
nephridia absent, large glandular mass (here
termed 'ventral glands') located under the nerve-
cord in XVII-XIX, spermathecae divided into a
subspherical ampulla and short, blunt digitiform

diverticulum bearing numerous sperm chambers
on its inner surface (*D. helonomia* diverges some-
what from this latter state).

It should be noted, however, that most of these
unifying characteristics are symplesiomorphies:
only the possession of pharyngeal tufting, genital
seta glands and ventral glands represent probable
synapomorphies.

Five new species of *Diplo-*
trema from south and
central Queensland were recently partly de-
scribed and sketched (Blakemore, 1997). Four of
these differ from the *fragilis* group in lacking
anterior nephridial tufting. A fifth, *D. ambrosen-*
sis, has anterior tufts, but, as for the other species,
the form and sculpturing of the penial, and geni-
tal, setae is not described, considerably impeding
comparison, and no reference is made to ventral
glands. As the penisetal follicles are described as
'enormous', it is unlikely that *D. ambrosensis*
belongs to the *fragilis* group.

KEY TO SPECIES OF THE *DIPLOTREMA*
FRAGILIS SPECIES-GROUP

1. Dorsal pores present 2
Dorsal pores absent
..... *D. proserpinensis* sp. nov.
2. Prostatic glands long, extending at least into seg-
ment XXI *D. fragilis* Spencer
Prostatic glands not extending beyond XX 3
3. Gizzard rudimentary; first dorsal pores in the vi-
cinity of 19/20; conspicuous glands associated
with the genital setae. *D. helonomia* sp. nov.
Gizzard well-developed; first dorsal pores in the
vicinity of 7/8; no conspicuous glands associ-
ated with the genital setae. *D. tyagarah* Dyne

***Diploptrema fragilis* Spencer, 1900**
(Fig. 1)

Diploptrema fragilis Spencer, 1900: 31-32 pl. 4, figs 4-6.

Diploptrema fragilis; Sweet, 1900: 114-5 pl. 14, fig. 6.

Diploptrema fragilis; Michaelsen, 1907: 142.

Plutellus (Diploptrema) fragilis; Michaelsen, 1916: 61.

Diploptrema fragilis; Jamieson, 1971: 100-102.

MATERIAL. Many specimens examined, 1 closely (condition poor). **SYNTYPES:** National Museum of Victoria G31. Approx. 25°37'S, 151°37'E., Gayndah, Sept., 1891-Qld.

DESCRIPTION. Length = 31mm. Width = 2.0mm. Segments = 111. Form cylindrical, anterior end blunt and rounded, slightly bulbous, pigmentless buff in alcohol. Prostomium closed, epilobous 1/2; first dorsal pore (perforate) in 9/10. Setae 8 per segment, closely paired, the ventral setal couples of XVIII present, those of XVII and XIX modified as enlarged penial setae, those of VIII and IX as genital setae. Nephropores not visible.

Clitellum annular, weaker ventrally, over XIII-XVI, dorsal pores obscured, intersegmental furrows and setae only sporadically visible. ♂ pores minute orifices equatorial, in XVIII. ♂ field an approximately circular, somewhat tumid area extending longitudinally from the setal arc of XVI to that of XIX, and laterally, in XVIII, beyond *b*-lines, small, indistinct, transversely oval papillae (the prostatic porophores) present in XVII and XIX, at the sites of the modified ventral setal couples. ♀ pores minute orifices in a pair of considerable papillae in front of *a* setae, on XIV. Spermathecal pores on a pair of elliptical, slender papillae, in 7/8, 8/9, with centres in *b*.

Accessory markings: a pair of horny ridges posteriorly in XIV, median to *a* (evidently misidentified by Spencer as the ♀ pores); a median transversely elliptical prominence in 17/18 is possibly a normal feature of the species. Segment VIII glandular, and appreciably widened.

Septa: 5/6 slightly, 6/7 and 7/8 moderately strongly, and 8/9 and 9/10 very strongly thickened, the succeeding three septa slightly thickened, remainder thin. Pharyngeal glands well-developed, forming several tiers of flattened, shortly palmate lobes in III, anteriorly. Dorsal blood vessel single, continuous to the posterior portion of the pharynx, flattened and adherent to the intestine in XIV posteriorly; last hearts in XIII, those of X-XIII large, and increasing slightly in size posteriorly, supra-oesophageal vessel present, but its limits not determinable because of maceration. Gizzard large, glossy, but thin-walled, in V. Oesophagus narrow, VI-XIV,

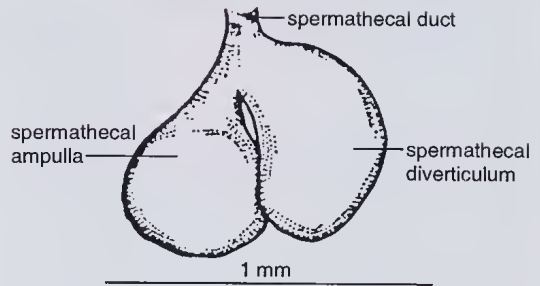


FIG. 1. *Diploptrema fragilis* Spencer, 1900. Right spermatheca of segment IX. Syntype (NMVG31).

calciferous glands or other elaborations absent; intestine commences with abrupt expansion in XV, reaching full width in XVI, a definite typhlosole lacking.

Nephridia exclusively holonephric, commencing in II, each invested in a high peritoneum and forming a regular, simple lobe on each side, in each segment; ducts long and avesculate, entering the parietes in *c*-lines. Pharyngeal tufting absent.

Holandric: large, thick-walled spermatic funnels present in X and XI; seminal vesicles 2 pairs of compact, lobulated, and fairly small masses in XI and XII. Prostatic glands 2 pairs of flattened, tubular organs, the anterior pair extending to XXII, the posterior set to XXIII. The glands are sinuous, with each bend contiguous with the next, ducts abruptly demarcated, slender, glossy, and running almost straight medianly. Anterior prostates approximately twice the size of the posterior pair, though the length of the ducts is similar; the ducts enter a median, internal glandular mass extending from XVII to XIX, and corresponding with the external manifestation of the ♂ field. Two penial seta follicles enter the glandular mass in the vicinity of the prostatic ducts, each with several setae; the setae slender, narrowly pointed, basally often expanded, gently curved or slightly sinuous, with the ectal 1/4 curved through as much as a right angle, the ectal end simple, or with a crumpled appearance; minute notching present on the shaft, mostly almost inappreciable. Length mature seta = 1.4mm (mean of 2), midshaft diameter = 40µm. Ovaries moderately stout, long, linguiform lobes of several large, irregularly arranged oocytes; funnels moderate-sized, simple, also in XIII. Spermathecae 2 subequal pairs, in VIII and IX, each with a medianly directed ovoid, or spherical ampulla and a lateral, equisized or somewhat longer, iridescent concavo-convex

diverticulum. The ampulla and diverticulum share a short narrow duct; length right spermatheca of IX (base of ampulla to pore) = 0.64mm. A battery of genital setae present in segments VIII and IX, located behind each spermathecal duct; the setae gently curving, with a broad point, ornamented with the deep, elongate, crescentic notching characteristic of such setae in acanthodrilids, from very near the tip to slightly less than halfway down the shaft, length mature seta = 9.98mm, midshaft diameter = 40µm (mean of 2).

REMARKS. There can be no doubt that the re-examined specimen is conspecific with the material described by Spencer (1900) as *Diplo trema fragilis*, the type of a new genus. The specimen presumably contributed to the description. Points of agreement in Spencer's account which confirm the identity of the re-examined specimen are: the epilobous prostomium, the large oval midventral glandular patch in XVI-XIX, and the swollen, glandular appearance of segment VIII. With respect to the position of the ♂ and prostatic pores, however, Spencer's account is erroneous, a departure from his usual accuracy, possibly because of the small size of the species. No credence can now be placed on his observation of only a single pair of prostates with pores behind the ♂ pores on XVIII; the re-examined specimen has two pairs of prostatic pores, on XVII and XIX, with the ♂ pores quite separate, on XVIII, as demonstrated by Jamieson (1971). The presence of an additional pair of prostatic glands was first noted by Sweet (1900) in her re-examination of *D. fragilis*, though she termed these prostates 'accessory glands'. All of the type-specimens, despite their poor condition which precludes illustration of the genital field, are clearly referable to a single species.

Accepting Spencer's original description, Michaelsen (1910) placed *D. fragilis* within a monotypic section of the Acanthodrilinae, the Diplo tremacea. A subsequent examination of New Caledonian species (Michaelsen, 1913) genuinely having the ♂ and prostatic ducts separate on XVIII (as erroneously described by Spencer, 1900, for *Diplo trema fragilis*), convinced Michaelsen that such an arrangement was closer to the plutelloid (and hence, Megascolecina) grade of organisation than to the acanthodrilin system. Accordingly, the latter species and *D. fragilis* were referred to a separate subgenus within *Plutellus*. The seemingly transitional condition of the ♂ terminalia in this group resulted

in the incorporation of *Plutellus* (*Diplo trema*) into a phylogenetic scheme (Michaelsen, 1916, 1921), endorsed and expanded by Stephenson (1930) where it occupied an intermediate position, separating '*Acanthodrilus*' from the truly megascolecina *Plutellus*. Stephenson adopted the term 'accessory prostates' for the organs illustrated by Sweet, while continuing to accept Spencer's original diagnosis for the genus.

After the true status of *D. fragilis* became known, the New Caledonian forms remained within the *Plutellus* congeries until accommodated within the newly erected genus *Eudiplo trema*. The uniqueness of the ♂ system in these species has thus been satisfactorily recognised (Jamieson & Bennett, 1979). The authors have attempted unsuccessfully to collect fresh material of *D. fragilis*, although a further quite distinct undescribed *Diplo trema* species was recovered by GD from the banks of the Burnett River at Gayndah, southeastern Queensland (SEQ).

Diplo trema helonoma sp. nov. (Figs 2, 3)

ETYMOLOGY. Latin, *helonoma*, a dweller in the marshes.

MATERIAL. (Holotype and 4 paratypes examined in detail) HOLOTYPE: ANICGD.95.144.1. BanBan Springs (25°41'S, 151°49'E), SEQ, in black swampy soil at and below the water table. Coll. G. Dyne and A. Postle, 9 June 1974: Numerous clitellates, immature specimens and fragments; PARATYPES: ANICGD.95.144.1, collection data as for holotype. FURTHER MATERIAL: ANICGD.95.144.1. Same locality, at side of spring, Coll. B. Jamieson and E. Bradbury, 21 May 1971: Numerous specimens (mostly a clitellate), not designated as type material.

DESCRIPTION. Length > 24mm, 113mm. Width (midclitellar) = 2.8mm. Segments ?, 182 (H – posterior amputee, P1). Pigmentless buff in alcohol, clitellum with a pinkish tinge, particularly in freshly preserved material. Prostomium epilobous 1/3, closed. First dorsal pore 19/20 (H, P1), dorsal pores generally indistinct. Setae regularly disposed in 8 rows, uniform in size with the exception of the ventral setae of XVII and XIX, which are enlarged as penial setae, and those of VIII and IX, modified as genital setae; ventral setal couples of XVIII present. Nephropores visible as minute depressions immediately anterior to *c* in each segment, by a distance slightly exceeding *cd*.

Clitellum annular, obscuring the intersegmental furrows, though the setae remain prominent; clitellum developed over 1/3 XII-XVI (more so

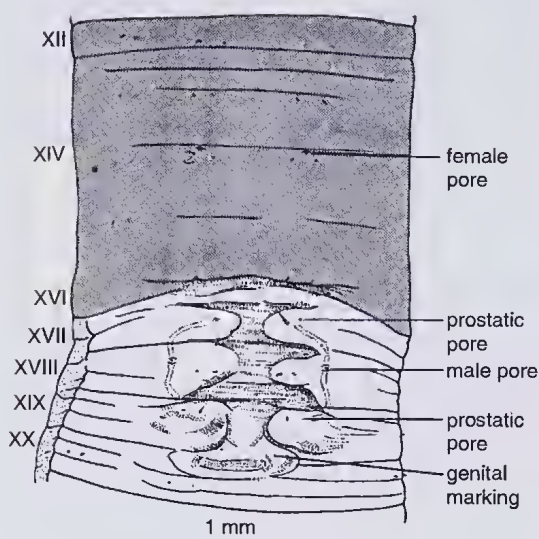


FIG. 2. *Diploptrema helonoma* sp. nov. Male genital field. Holotype (ANICGD.95.144 I).

dorsally, where it extends to beyond 1/2 XVII). ♂ pores 2 orifices at the midpoints of a pair of narrow, ill-defined (shallow) seminal grooves linking the prostatic porophores of a side; the ♂ pores are located barely presetally on XVIII, in *bc*, closer to *b*. Dependent on the state of muscular contraction during fixation, the ♂ field (defined laterally by the seminal grooves, anteriorly by a rhomboidal tumescence, and posteriorly by another marking), may be either generally concave, which sharpens the relief of the porophores, and the ridge joining the ♂ pores, or of fairly uniform contour. The former condition is presumably assumed during copulation, when the genital orifices would need to be raised for adpression to a partner. The porophores are coincident with the penial seta openings; the setae may be protruded in preserved specimens (H, P4), or withdrawn (P1, P3); in the former case, each porophore would appear to have only a single seta protruding at any one time. ♀ pores a pair of pre-setal slits, roughly aligned with *ab*, on XIV. Spermathecal pores 2 pairs in 7/8 and 8/9, each with a prominent presetal lip, and with posteriorly adjacent tumescences associated with the genial seta follicles.

Accessory markings: a large, unpaired median rhomboidal (or elliptical) swelling in 16/17 (developed to a greater or less extent in all clitellate specimens examined); a similar marking in 19/20; the ♂ field (divisible into 4 depressed

areolae in contracted specimens) is also glandular, occasionally (P4), with pore-like impressions. Septa: 5/6 thickened, 6/7-9/10 moderately muscularised, remainder thin. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, the commissurals in X-XIII large, and latero-oesophageal; the supra-oesophageal vessel is traceable from VI to XIV, attaining maximal size in VI-IX, where its increased importance apparently corresponds to a decline in the size of the dorsal vessel. The remaining commissurals decrease in size anteriad, and are dorso-ventral only. Gizzard small, soft and readily compressed, though with a slight muscular sheen, in V; oesophagus moderately wide, vascular, in VI-XVII, calciferous glands or conspicuous outpouchings absent. Intestinal origin in XVII, dilating gradually posteriorly, typhlosole lacking.

Holonephric: nephrostomes conspicuous on long necks in *ab*; avesculate ducts open in line with *c*-setae, entering the parietes slightly anterior to the setal arc; nephridial bodies are enveloped in thin peritoneum, appearing as regular wafer-like units in each segment. Anterior tufting is absent.

Holandric: 2 pairs of brightly iridescent spermathecal funnels are present in X and XI, and 2 pairs of large, acinous seminal vesicles in IX and XII, the latter pair conspicuously the larger, and occupying virtually the entire ventral portion of that segment. Prostatic glands 2 pairs of coiled, tubular organs which encroach on posterior segments to a greater or lesser degree, penetrating the septa. The anterior pair is always the larger of the two. The prostatic ducts are short, straight and slightly muscular. The entire prostatic region is covered ventrally with a glandular mass that appears to be an internal manifestation of the ♂ field, and which may be responsible for secretions necessary for successful copulation. The prostatic ducts and penisal follicles pass through this mass prior to discharging to the exterior. Penisal follicles (consisting of conjoined *a* and *b* setal components) are equipped with little copulatory musculature; the setae are moderately long and gently arcing, the ectal 1/8 ornamented with irregularly spaced, rounded, deep scallops of variable diameter with somewhat jagged overhangs; these become more scattered and shallower entally. Length of mature setae = 1.9 mm, midshaft diameter = 36.2 µm (mean of 3).

Ovaries, consisting of flabelliform clusters of oocytes, and medium-sized ovarian funnels, present in XIII; no ovisacs demonstrable. Spermathecae 2 subequal pairs in VIII and IX,

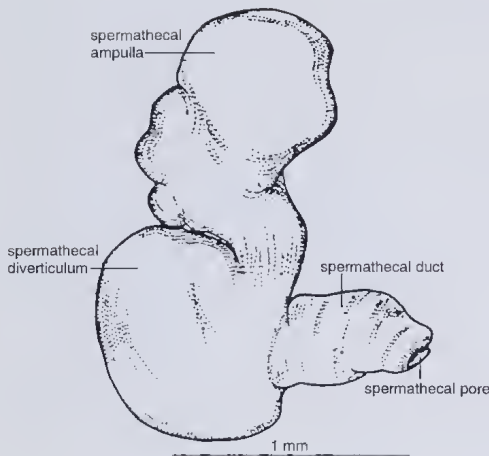


FIG. 3. *Diplotrema helonoma* sp. nov. Left spermathecal of segment IX. Paratype 1.

discharging anteriorly in their segments; each consisting of a bipartite ampulla: a clavate or irregular sacciform portion, connected by a broad neck to a subspherical component. A small, hemispherical 'diverticulum' is sessile on the latter, opposite to the point of attachment of the clavate section of the ampulla; a medium-sized duct is shared by the ampulla and diverticulum; the latter is brightly iridescent, containing numerous intramural sperm chambers. Length right spermatheca of IX = 1.7mm (base of ampulla to pore). Conspicuous genital seta follicles are associated with the spermathecae; these are surrounded by prominent, discrete, whitish glands, of which there is one per follicle in IX, and two in VIII. These glands are prostate-like, both in overall morphology and histologically, with a definite central lumen leading to small ducts discharging at the point of emergence of the genital seta from the body wall; their function is unknown. The setae are fairly straight, ornamented over the ectal portion of the shaft (including the somewhat swollen apical region) with conspicuous longitudinal fluting; this appearance is due to the alignment of long roughly parallel scallops with fairly smooth edges. Length of mature seta = 1.34mm; midshaft diameter = 35.1µm (mean of 3).

REMARKS. *Diplotrema helonoma* is the geographically closest species to *D. fragilis*. The similarities in overall morphology shared by the two taxa leaves little doubt as to their phylogenetic propinquity. Points of divergence include the much reduced gizzard in *D. helonoma*, differ-

ences in the position of the seminal vesicles and the dorsal pores and the conspicuous development of genital seta glands in *D. helonoma*.

***Diplotrema proserpinensis* sp. nov.**
(Figs 4, 5)

ETYMOLOGY. Named for the type locality.

MATERIAL. HOLOTYPE: QMG5449. Myrtle Creek, between Cannonvale and Proserpine, (20°23'S, 148°36'E), CEQ; frequent in mud in the bottom of and in the bank of a stagnant backwater. Coll. B.G.M. Jamieson, 15 Jul 1966. PARATYPES 1-3: QMG2887, 2892, 2893, collection data as for holotype. OTHER MATERIAL: QMLGH2888, collection data as for holotype.

DESCRIPTION. Length = 103, 82mm. Width = 1.5mm. Segments = 225, 175 (H, P1). Form cylindrical, anterior end slightly bulbous over several segments, pale in alcohol. Prostomium pro-epilobous, dorsal pores absent. Setae closely paired throughout, ventral setal couples of XVIII present, those of XVII and XIX modified as enlarged penial setae, often protruding through the prostatic pores; those of VIII replaced by genital setae, situated on strongly protuberant papillae. Nephropores not externally recognisable.

Clitellum not developed. ♂ pores seen slightly presetally, lateral of *b*-lines, in shallow seminal grooves that link the porophores of a side; prostatic pores 2 pairs, on medianly inclined dome-shaped papillae at the *ab* loci of XVII and XIX. The ventral body surface is depressed within the area circumscribed by the four prostatic papillae and extending as far as intersegment 16/17 and 19/20, its margins raised on each side as a longitudinal ridge along which the seminal grooves run. ♀ pores minute, presetal in *a* or *b* lines of XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, seen as elliptical areas, in *b*-lines.

Accessory markings: large, glandular pad, approximately circular in outline occupies most of XX between the *a* setae, and encroaches somewhat into XIX. This marking is developed only in the holotype to any significant degree, very faintly in P1, and not seen in any other specimens examined.

Septa: none strongly muscularised, but those anterior to and excluding 9/10 somewhat thickened. Dorsal blood vessel single, last hearts in XIII; of all the commissurals in VII-XIII, only those in XII and XIII are large and heart-like. Further vascular details not determinable owing to the small size of the species and pronounced bleaching. Gizzard large, in V; oesophagus narrow, moniliform, in VI-XIX, lacking pouching or

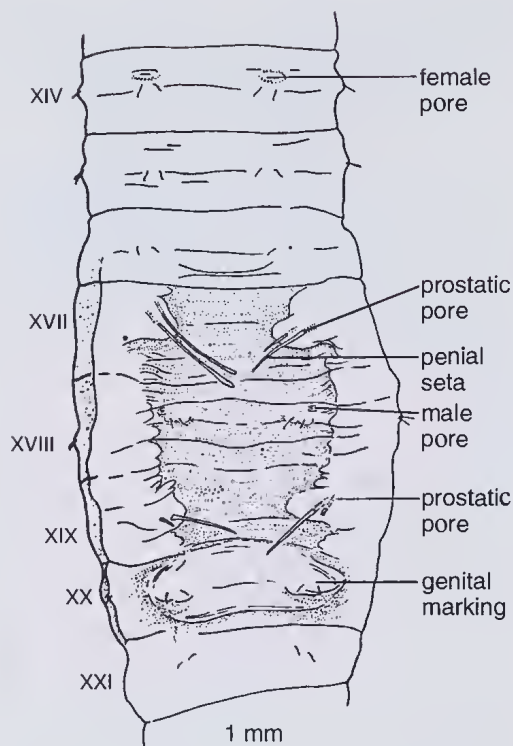


FIG. 4. *Diplotrema proserpinensis* sp. nov. Male genital field. Holotype (QMG5449).

calciferous glands. Intestine commences in XIX or XX, a well-developed oesophageal valve present at 18/19 or 19/20; typhlosole absent.

Nephridia present at least as far forward as VIII, stomate, their avesiculate ducts entering the parietes in a single series on each side, in *c*-lines; pharyngeal tufting absent.

Holandric: 2 pairs of very large, iridescent spermatic funnels, and sperm masses, free in X and XI; seminal vesicles lobed, in XI and XII, those of XII filling the segment longitudinally, those of IX smaller. Prostatic glands slender tubes, those of XVII slightly tortuous, and extending into XIX or XX; those of XIX much smaller, tortuous, extending into XX; each with a slender duct. Penisetae well-developed, each extending into its next posterior segment, four or more setae to a bundle. The setae curved gently, or through as much as a semicircle, ornamented over the distal sixth by a series of widely-separated, minute, distally directed teeth, some or all of which are members of transverse circlets; the distal extremity of the setae are 'laterally' widened, and terminally form a bulb with or without a small, apical point. Length

mature seta = 0.75mm, midshaft diameter = 27.3 μ m (mean of 2).

Ovaries, each with several strings of large oocytes, and funnels, present in XIII, ovisacs absent. Spermathecae two pairs, in VIII and IX, the posterior pair almost twice as large as the anterior. Each with a large, somewhat irregular ampulla, and a stout duct, at the ectal end of which, medially, is a single, large, ovoid diverticulum which may be almost as large as the ampulla. Length left spermatheca of IX = 0.66mm. Large genital seta follicles present in VIII, apparently associated with a glandular manifestation; the setae fairly straight, the ectal 1/3 ornamented with a series of longitudinal scallops, giving a serrated appearance. Length mature seta = 0.75mm (mean of 3), midshaft diameter = 27.3 μ m.

REMARKS. The absence of dorsal pores in this species may be connected with its semi-aquatic mode of existence, since this loss is also seen in the primarily limnic families Alluroididae, Biwadrilidae, Almidae, Lutodrilidae, Sparganophilidae and the marine littoral megascolecid *Pontodrilus* (see Jamieson, 1988). It is presumably a response to the superfluity of coelomic fluid lubrication in aquatic habitats. *D. cornigravei*, which also lacks dorsal pores, is not necessarily related to members of the *D. fragilis* species-group. The disappearance of dorsal pores in the former species, recorded 'from swampy ground' (Jackson, 1931), has probably occurred convergently.

Whereas the gut contents of *D. helonoma* consist almost entirely of soft, partially digested organic matter, the upper alimentary tract of *D. proserpinensis* was found to contain, inter alia, numerous irregular quartz grains (especially in

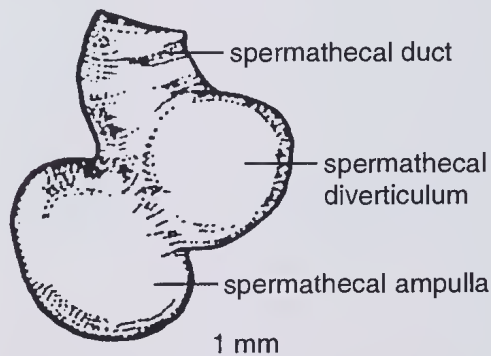


FIG. 5. *Diplotrema proserpinensis* sp. nov. Left spermatheca of segment IX. Holotype (QMG5449).

the gizzard). A dietary divergence may therefore account for the differential development of the gizzard in the two species.

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FIRST RECORD OF BULLER'S ALBATROSS IN QUEENSLAND. *Memoirs of the Queensland Museum* 42(2) 494. 1998:- Buller's Albatross (*Diomedea bulleri* Rothschild, 1893) has not previously been documented from Queensland (Blakers et al., 1984; Storr, 1984; Lindsey, 1986; Marchant & Higgins, 1990), and is not represented in the collections of the Queensland Museum (S. Van Dyck, pers. comm.). Furthermore, to our knowledge, no sight records of the species exist for the State. We report here the first Queensland record of *D. bulleri*, based on a description and skull of a beach-washed specimen from North Stradbroke I., SEQ.

During 1991, a dead albatross was found stranded on Frenchmans Bch, Point Lookout (27°25'S, 153°32'E) by a local resident, G. Blackburne. The collector examined the bird, which was in fresh condition, then removed the head to assist with identification. Features noted, including a grey head and yellow upper and lower bill margins, matched those described by Simpson (1976) for Buller's Albatross (G. Blackburne, pers. comm.). [Although a separate account of *D. bulleri* does not appear in this publication, distinguishing characters for the species are provided in the text for the Grey-headed Albatross (*D. chrysostoma* Forster, 1785)]. Notes detailing the appearance of the bird's plumage and bare parts were not made, but the skull, without its bill plates, was retained.

The skull was shown to ICG during May 1993, by which time the collector could not recall the exact date of the find. Because of its significance, the specimen was subsequently obtained and registered in the Queensland Museum as O30971. To confirm the original identification, it was forwarded to the Museum of New Zealand (MNZ) for comparison with skulls of the four Australasian mollymawk species in the same general size range, namely Buller's, Grey-headed, Yellow-nosed (*D. chlororhynchos* Gmelin, 1789) and Black-browed (*D. melanophris* Temminck, 1828) Albatrosses. The Point Lookout skull matches specimens of Buller's Albatross well. It is larger than *D. chlororhynchos* skulls, and of the two other species similar in size and shape to O30971, the skull of *D. chrysostoma* is usually larger again and possesses a flat section along the top of the culmen, whereas that of *D. melanophris* has larger nasal entrances and smaller orbital ridges (A. Tennyson, in litt., 3.10.97).

Buller's Albatross, a non-breeding migrant from New Zealand, has been recorded often in SE Australia (Lindsey, 1986; Marchant & Higgins, 1990), but is considered to be uncommon

off the east coast N of Eden (37°04'S, 149°54'E; D.W. Eades in Marchant & Higgins, 1990). Holmes (1977) documented two birds off Coff's Harbour (30°18'S, 153°09'E) from 1974-1976, and Lindsey (1986) states *D. bulleri* is known N to Byron Bay, NSW (28°38'S, 153°38'E) but provides no details of specific records. The beach-washed specimen from Point Lookout thus extends the species' distribution further northward. That *D. bulleri* would eventually be added to Queensland's avifauna was not unexpected given the relatively close proximity of its reported occurrence in northern NSW. The timing of available records from this region, e.g., June and July in Holmes (1977), suggests Buller's Albatross may be an occasional winter straggler to southern Queensland.

Acknowledgements

Geoff Blackburne kindly provided the Buller's Albatross skull and information about his initial discovery. The efforts of Alan Tennyson, Collection Manager (Birds) at the MNZ, in verifying the identity of the skull are greatly appreciated. We thank Rory O'Brien (Museum of Victoria) for comments on the manuscript.

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BRYORACHIS (PHIDOLOPORIDAE) AND *RETELEPRALIA* (CHEILOPORINIDAE):
TWO NEW GENERA OF INDO-PACIFIC BRYOZOA

DENNIS P. GORDON AND PETER W. ARNOLD

Gordon, D.P. & Arnold, P.W. 1998 06 29: *Bryorachis* (Phidoloporidae) and *Retelepralia* (Cheiloporinidae): Two new genera of Indo-Pacific Bryozoa. *Memoirs of the Queensland Museum* 42(2): 495-503. Brisbane. ISSN 0079-8835.

Two new genera of ascophorine Cheilostomatida are recognised from northeastern Australia and the Norfolk Ridge. *Bryorachis* (family Phidoloporidae), with erect, unbranching or scarcely branching stems, has a colony form somewhat intermediate between that of *Reteporellina* and *Chevron*. Two species, both new, are ascribed to *Bryorachis*. *Retelepralia*, with a sole included species, also occurs in Mauritius. Provisionally included in the Cheiloporinidae, it is characterised by relatively large, ventricose zooids interconnected by short tubular processes. There is also a striated median gymnocystal strip frontally. □ *Bryozoa*, *Bryorachis*, *Retelepralia*, *taxonomy*, *deep-sea*.

Dennis P. Gordon, National Institute of Water & Atmospheric Research (NIWA), P.O. Box 14-901 Kilbirnie, Wellington, New Zealand; Peter W. Arnold, Museum of Tropical Queensland, 70-84 Flinders Street, Townsville 4810, Australia; 31 March 1997.

In the course of the authors' respective studies on the bryozoan faunas of the Norfolk Ridge and NE Australia, recent collections from deeper water have yielded new taxa common to both areas. These comprise two new species representing a new genus of the lace-coral family Phidoloporidae, and a third species, previously known only from Mauritius, representing a new genus of Cheiloporinidae.

The new phidoloporid genus is only the second in the family occurring on soft sediments and appears significant in its unique colonial morphology as transitional between a shelf/slope genus of rigid-erect species and a deep-sea genus whose species are found on terrigenous-foraminiferal oozes. The new cheiloporinid is unusual in the family, and among lepralioid ascophorines generally, in having encrusting zooids linked by tubular connections.

The purpose of this paper is to describe the new taxa, and assess their taxonomic and biogeographic affinities.

MATERIALS AND METHODS

Material was collected in the course of various oceanic cruises. Specimens from the Norfolk Ridge were collected during cruises of New Zealand Oceanographic Institute (NIWA) research vessels Taranui and Tangaroa. Specimens from the Coral Sea were collected during three *Cidaris* expedition cruises of R.V. Franklin.

Selected specimens were soaked in domestic bleach (hypochlorite solution) to remove organic tissues from the zooidal skeletons. These were

washed thoroughly in water and dried prior to carbon or gold coating for scanning electron microscopy.

Dimensions were calculated from the scale bars in SEM photographs and checked by calibration against graticule measurements using light microscopy.

SYSTEMATICS

Class GYMNOLAEMATA Allman, 1856
Order CHEILOSTOMATIDA Busk, 1852
Family PHIDOLOPORIDAE Gabb & Horn, 1862

Bryorachis gen. nov.

ETYMOLOGY. The generic name is derived partly from the phylum name *Bryozoa*, and *rachis*, a Greek feminine noun meaning backbone, alluding to the appearance of the stems.

TYPE SPECIES. *Bryorachis pichoni* sp. nov.

DIAGNOSIS. Colony erect, rod-like and unbranched, or with limited branching basally and laterally, with distinct frontal and abfrontal surfaces. Stems 3-5-serial, the axial and adjacent longitudinal series of zooids opening frontally, additional series originating abfrontally but directed laterally. Zooidal peristomes projecting, the paired lateral ones giving the stems the appearance of vertebral columns; peristomial orifices lack spines but may be denticulate. Primary orifices suborbicular with a broad shallow sinus, the distal arch beaded. Autozooids with a depressed granular-tubercular area frontally in which a pair of areolar pores are recessed proximally. Avicularia absent from the axial row of zooids, present adventitiously on most of the

others except at proximal ends of stems, with short rounded or triangular rostrum. Ovicells cucullate, smooth and imperforate, widely open frontally and non-labellate. Abfrontal kenozooids small, disposed at regular intervals adjacent to the dorsal walls of the lateral zooids and often bearing small avicularia.

***Bryorachis pichoni* sp. nov.**
(Figs 1, 2A,B)

ETYMOLOGY. For the chief scientist on the Cidar expedition, Professor Michel Pichon (École Pratique des Hautes Études, Université de Perpignan, France).

MATERIAL. HOLOTYPE: QMG21274, J-shaped colony, Cidar 3 Stn 6.4, 11 Nov. 1992, 10°00.82'S, 145°00.15'E, 1777m, Calypso dredge, coll. M. Pichon, R.A. Birtles, P.W. Arnold, in alcohol. PARATYPES: QMG21275, L-shaped colony, same locality as holotype, mounted on SEM stub; QMG21276, 4 additional fragments, in alcohol. ADDITIONAL MATERIAL: Cidar 1 Stn 20.3, 10 May 1986, 17°46.5'S, 147°48.8'E, 1223–1224m, Ockelmann epibenthic sledge, coll. M. Pichon, R.A. Birtles, P.W. Arnold, 1 specimen in alcohol (QMG21277), 1 mounted on SEM stub (QMG21278). Cidar 1 Stn 35.1E, 13 May 1986, 16°50.7'S, 147°08.1'E, 1604m, Smith-MacIntyre grab, coll. M. Riddle, D. Alongi, 1 specimen in alcohol (QMG21279). Cidar 3 Stn 6.3, 11 Feb. 1992, 10°01.2'S, 145°01.5'E, 1777–1779m, Ockelmann epibenthic sledge, coll. M. Pichon, R.A. Birtles, P.W. Arnold, 1 specimen mounted on SEM stub (QMG21280).

DESCRIPTION. Colony (known only from fragments) erect, rod-like, maximum length 8.0mm, generally unbranched but limited branching basally can create roughly L- or J-shaped colonies; 1 colony has a short lateral branch. Stems 3–5-serial, 0.54–0.69mm wide between peristomial projections, 1.9–2.5mm at peristomial projections.

Zooids in the axial longitudinal row 0.89–0.98mm long and 0.33–0.52mm wide. Frontal shield in these zooids with an extensive granular-tubercular depressed area, 0.38–0.53mm long and 0.21–0.33mm wide, at the proximal end of which is a pair of recessed areolar pores, 0.06–0.09mm wide, best seen in oblique view. Peristomes sub-tubular, projecting, especially in lateral zooids, the secondary orifice 0.23–0.27mm diameter with an irregular rim; with labial pore (spiramen) and

median suture inset in a groove. Primary orifice suborbicular, the distal arch of the anter beaded, with broad sinusoid poster; no condyles. Autozooids flanking axial series of zooids similar to them but the granular-tubercular area not significantly depressed and lacking areolar pores, the orifices facing about 40° away from main axis; both these zooids and the axial ones bear ovicells. Most lateral autozooids originate abfrontally at an oblique angle but the peristomes on each side are directed laterally in opposite pairs; labial pore and groove visible frontally, but also with a distinct groove and pore abfrontally; not seen to bear ovicells.

Ovicells recumbent, cucullate, 0.25–0.35mm long and 0.28–0.35mm wide, smooth and imperforate and widely open frontally; no labellum or lateral slits but the sides of the ovicell descending somewhat proximally.

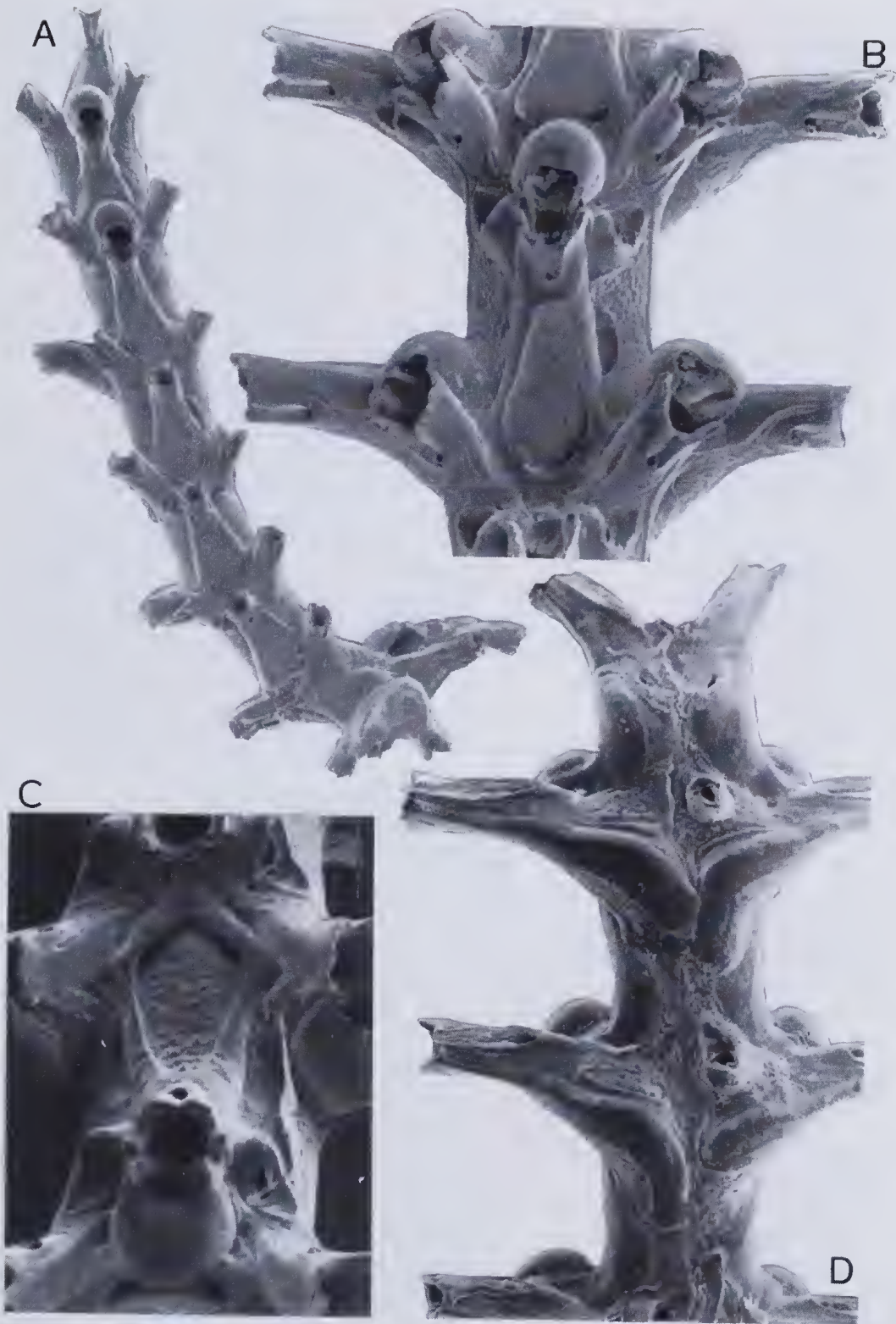
Avicularia adventitious, borne mostly on the zooids flanking the axial series, occasionally on the most lateral zooids, never on the axial ones; somewhat oval in shape with a variable rostrum (rounded-triangular to acute) and complete cross-bar, positioned adjacent to the peristomes of the axial autozooids.

Abfrontal kenozooids roughly triangular, infilling axillary region between dorsal walls of autozooids; surface granular, usually with 2 small pores and occasionally an avicularium like the frontal ones.

Ancestrula with globular base, orientated at right angles to main growth axis. Peristomes of the first 3–5 zooids (including ancestrula) directed to base of colony, with a reversal in orientation of subsequent zooids to form a single growth axis or short branches.

REMARKS. Among the various specimens taken at different stations, the most significant variation is in the form of the avicularia. Specimens from Cidar 1 Station 20.3 (17°46'S, 1223–1224m) have more acutely triangular mandibles on both frontal and abfrontal surfaces than in specimens from Cidar 3 Stations 6.3 and 6.4 (c. 10°01'S, 1777–1779m). The opesial region of the avicularium is contained in a more prominently exerted base in specimens from Cidar 1 Stn 20.3.

FIG. 1. A–D, *Bryorachis pichoni* gen. et sp. nov. (registered material from the Coral Sea). A, frontal view of L-shaped paratype colony (QMG21275), $\times 23$. B, central part of stem with ovicelled zooids, $\times 44$. C, frontal view, tilted to show the characteristic paired proximofrontal areolar pores, $\times 63$. D, abfrontal view of distal end of stem showing arrangement of peristomes and avicularia, $\times 37$; (B–D, QMG21278).



***Bryorachis curiosa* sp. nov.**
(Fig. 2C,D)

MATERIAL. HOLOTYPE. NIWA (N.Z. Oceanographic Institute) registration no. H-671, from NZOI Stn G10, 32°09.5'S, 168°15.0'E (southern part of Norfolk Ridge NE of Wanganella Bank, just inside the Australian EEZ of Norfolk I.). 970m, coll. 29 Sept. 1966 during the Noumea Cruise of R.V. Taranui. Only known specimen, coated frontally for SEM examination.

DESCRIPTION. Colony erect, rod-like, unbranched, the sole fragment 6.0mm long, the proximal end rounded. Stem 5-serial, 0.65-0.71mm wide between peristomial projections, 1.19-1.50mm at peristomial projections.

Autozooids in the axial longitudinal row 0.77-0.94mm long. Frontal shield of these zooids with a conspicuous granular-tubercular depressed area, 0.33-0.39mm long and 0.27-0.36mm wide, at the proximal end of which is a pair of recessed areolar pores each up to 0.09mm wide, visible frontally but especially conspicuous when viewed obliquely. Zooidal peristomes subtubular, scarcely evident on the axial zooids, most developed on the lateral ones, the secondary orifice 0.22-0.24mm wide with a U-shaped pseudosinus that is not further constricted to become a closed labial pore and suture. Primary orifice suborbicular, the distal arch of the anter beaded, with broad sinusoid poster; no condyles. Autozooids flanking axial autozooids similar to them, granular-tubercular over most of the surface but lacking the depressed area and areolar pores; peristomes facing slightly away from main axis.

Ovicells not present. Avicularia adventitious, borne on most autozooids except the axial series, with a very narrow opesia region separated by a complete crossbar from the rounded rostrum; positioned adjacent to the peristomes of the axial autozooids.

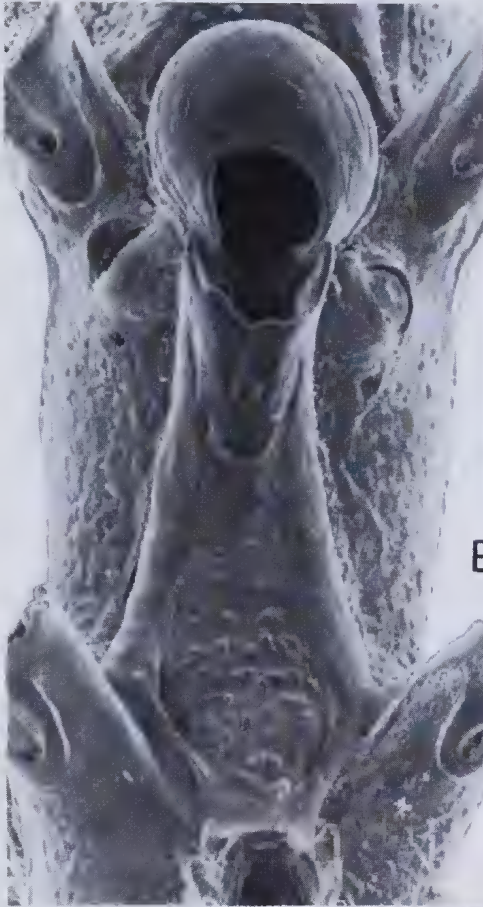
Abfrontal surface granular-tubercular; kenozooids somewhat pyriform to rounded-triangular, situated on the 'backs' of the most lateral zooids, adjacent pairs of kenozooids separated by an irregularly zigzag median groove coursing down the back of the stem. Each kenozooid typically with an avicularium identical to the frontal ones.

REMARKS. The sole colony fragment of *B. curiosa* is somewhat worn, and lacked membranes and soft tissue when collected. It may have been transported; the peristomes of all the zooids are eroded distally, although it appears that the peristomes of the axial series of autozooids did not project as far in life as those of the marginal zooids. Despite the condition of the specimen, it is clearly congeneric with *B. pichoni*. Both species share the following characteristics: same colony morphology, i.e., having the appearance of a vertebral column; the axial series of autozooids lack avicularia and have a depressed frontal area with two proximal areolar pores; regularly disposed abfrontal kenozooids with adventitious avicularia; same shape of primary orifice.

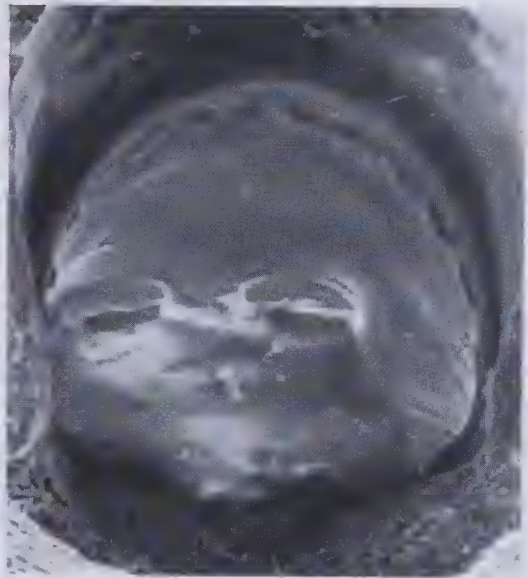
Bryorachis curiosa differs from the type species in having a rounder, more conspicuous depressed area frontally, in some zooids bordered by an inner rim; one zooid has two depressed areas in one and it appears that this and the bordering rims in other zooids are the product of some kind of frontal budding, although for what purpose is unclear. It is conceivable that 1-2 rhizoids could issue from the areolar pores, descend basally, and anchor the colony to the substratum, but we have no evidence of rhizoids in either species. Other differences between the two species include the lack of a closed labial pore in *B. curiosa* and rounder avicularian rostra.

ECOLOGY. *B. curiosa* is known from only one station, at 970m depth on the southern part of the Norfolk Ridge NE of Wanganella Bank. The sole specimen was taken in a 10-min pipe-dredge sampling which yielded a meagre collection of sand and gravel with pteropod shells, stylasterid hydroids, solitary corals, and bryozoan fragments. Notwithstanding the small size of the collection, the many broken fragments give evidence of an impressive diversity of erect growth forms among the several genera of stylasterids and bryozoans. The latter include *Crassimarginatella vincularia* Gordon (Calloporidae), *Nellia tenella* (Lamarck) (Quadricellariidae), *Bryopastor* sp. (Chaperiidae), *Poricellaria* sp. (Poricellariidae), *Atelestozoum* sp., *Cellaria* spp., *Euginoma* sp., *Syringotrema* sp. (Cellariidae), *Siphonicytara* sp. (Siphonicytaridae), *Raxifabia* sp. (Bifaxariidae).

FIG. 2. A-B. *Bryorachis pichoni* gen. et sp. nov. (registered material from the Coral Sea). A, close-up of ovicelled zooid (QMG21275), $\times 95$. B, primary orifice, showing blunted distal beading and the shallow arcuate proximal rim, $\times 492$. C-D. *Bryorachis curiosa* gen. et sp. nov. (registered material from NIWA Stn G10, Norfolk Ridge). C, part of transported stem showing arrangement of zooids and the subcircular depressed area of an axial zooid with a secondary rim from apparent frontal budding, $\times 70$. D, entire transported stem, $\times 17$; (C-D, NIWA holotype H-671).



B



A



C



D

dae), *Plagiopora recens* Gordon (Catenicellidae), *Kladapheles gammadeka* Gordon (Lepraliellidae), *Mawatarius inexpectabilis* (Gordon), *Mawatarius* sp. (Mawatariidae), and an undescribed genus of Celleporidae. The only encrusting or nodular bryozoans were species of *Smittina* (Smittinidae) and *Celleporina* (Celleporidae). The diversity of erect forms anchored by rootlets probably reflects the primarily unstable soft-sediment habitat. The few encrusting or nodular species would be limited to small areas provided by gravel particles, pteropod shells, and fragments of corals and bryozoans.

Family CHEILOPORINIDAE Bassler, 1936

Retelepralia gen. nov.

ETYMOLOGY. The name is constructed of rete, a Latin neuter noun meaning net or network, and Lepralia, a well-known abandoned genus of cheilostomate bryozoans from which the adjective lepralioid is derived.

TYPE SPECIES. *Lepralia mosaica* Kirkpatrick, 1888.

DIAGNOSIS. Colony encrusting, tending to pluriserial. Autozooids large, linked quincuncially by short tubular processes. Frontal shield lepralioid, highly convex, evenly and densely pseudoporous, with or without a smooth thin ridge in the midline longitudinally. Orifice distinctly divided into anter and poster, the latter broad, straight or barely convex, separated from anter by a pair of stout condyles. No oral spines. No avicularia. Ovicells relatively short, endooecium granular-tubercular and imperforate, ectooecium membranous, the combined orifice larger than that of autozooids and closed by the zooidal operculum.

Retelepralia mosaica (Kirkpatrick, 1888) (Fig. 3A-D)

Lepralia mosaica, Kirkpatrick, 1888: 79, pl. 8, fig. 6.
Hippopodina mosaica, Hayward 1988: 319, fig. 6a,b.

MATERIAL. NIWA: A small infertile colony from NZOI Station 190, 29°25.0'S, 168°05.6'E, Norfolk Ridge SE of Phillip I., 71m depth, coll. 23 July 1975 during the Norfolk Ridge Cruise of R.V. Tangaroa. Museum of Tropical Queensland: QMG21281, a relatively large fertile colony on SEM stub, from RV. James Kirby Stn 1467, 18°57'S, 146°58'E, mid-shelf, central Great Barrier Reef, 24m depth, coll. 9 Aug. 1986 using Ockelmann epibenthic sled by R.A.

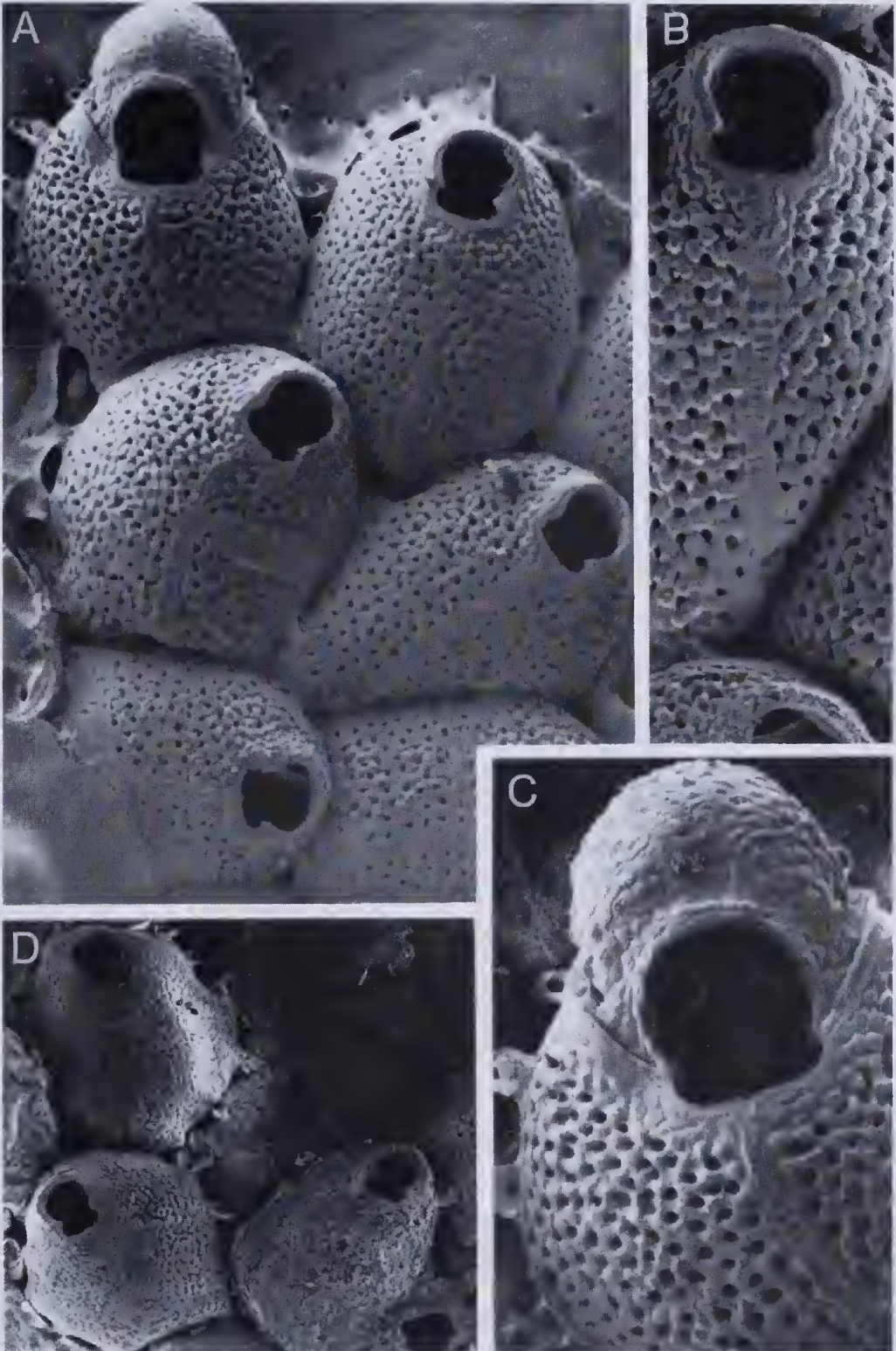
Birtles and P. Arnold. The Natural History Museum, London, BMNH reg. no. 1934.10.6.20, *Lepralia mosaica* Kirkpatrick, 1888, from Mauritius.

DESCRIPTION. Colony encrusting, forming relatively small planar patches less than 1 cm across, the zooids generally arranged quincuncially or, depending on the substratum, somewhat pluriserially. Zooids large, 0.77-0.92mm long and 0.57-0.72mm wide, each connected to its neighbours by c. 5-7 short tubes around the latero-proximal margins basally; these separated by uniporous septula from the parent zooids. Frontal shield lepralioid-cryptocystidean, densely and evenly pseudoporous with small tubercles between the pores; the shield arching convexly from the midline to join the basal wall on each side laterally; at the place where the frontal and basal walls meet may be a slight gymnocystal ridge, representing a thin, upwards extension of the basal wall. This ridge is continuous with a thin median strip of calcification that extends along the midline of each zooid towards the orifice; a series of transversely parallel ridges and grooves may occur along the median strip.

Orifice longer (c. 0.18mm) than wide (c. 0.15mm), with a large, evenly rounded anter separated from a broad poster by a pair of stout condyles, the proximal rim of the poster gently convex or nearly straight. The orificial rim comprises a thin gymnocystal strip that is continuous with the one in the zooidal midline. No oral spines. No avicularia.

Ovicell subglobose, relatively small compared to the overall volume of the autozooid, the endooecium granular-tubercular and imperforate, the ectooecium membranous. The frontal opening of the ovicell larger than autozooidal orifices, widely arching above the anter of the maternal zooid such that its sides extend to the level of the condyles; thus the ovicell is fully sealed when the zooidal operculum is closed. The edge of the opening and the lateral margins of the ovicell are bordered by a thin gymnocystal strip where the membranous ectooecium attaches that parallels another on each side of the orifice coursing distolaterally to the edge of the zooid. The ovicell illustrated (Fig. 3A,C) was raised and free of the substrate on a terminal autozooid so there could

FIG. 3. A-D, *Retelepralia mosaica* (Kirkpatrick). A, several zooids of a colony, including one ovicelled zooid at the colony margin, $\times 67$. B, close-up of a zooid showing well-developed striations along the median strip, $\times 10$. C, close-up of ovicellular endooecium and fertile orifice, $\times 123$ (A-C, QMG21281 from mid-shelf, GBR). D, three zooids, one quite worn, $\times 42$ (unregistered colony from NIWA Stn 190, near Phillip I., Norfolk Ridge).



be no contribution to the frontal shield of the ovicell from a distally placed autozoid.

Ancestrula unknown.

REMARKS. Examination of part of Kirkpatrick's Mauritian material of *Lepralia mosaica* demonstrates conspecificity with our specimens. Whereas neither Kirkpatrick (1888) nor Hayward (1988) illustrated or mentioned the median gymnocrystal strip on the frontal shield, it is nevertheless present in the loaned Mauritian specimen. In zooids in which the outer epitheca is present, however, it can be difficult to detect, which explains its not having been noticed previously.

ECOLOGY. No information is available on the provenance of Kirkpatrick's material other than that it was collected from Mauritian waters. In the Australasian region, *Retelepralia mosaica* occurs at shallow shelf depths. At NZOI Stn I90 SE of Phillip I., *R. mosaica* was taken at 71m depth by a medium Agassiz trawl from a bottom of biogenic rubble dominated by a species of pectinid bivalve, with octocorals, gastropods and hermit crabs, *Asterodiscus* (Asteroidea), and a variety of echinoids. The sole colony of *R. mosaica* encrusts bryozoans and foraminiferans on a shelly substratum. The Barrier Reef material was collected from soft sediment with calcareous green algae, coralline-algal rhodoliths, seagrass, and extensive biogenic rubble. The site had the greatest species richness and species diversity of molluscs and echinoderms of any along a cross-shelf transect (Birtles & Arnold, 1988). *Retelepralia mosaica* grew on the skeleton of a discoidal foraminiferan *Marginopora vertebralis* de Blainville, which was also overgrown by an unidentified cyclostomate bryozoan and cheilostomate bryozoans of the genera *Trypostega* and *Exechonella*. The similarity of habitats between the GBR and NZ sites, particularly, and the failure to recollect *R. mosaica* on coral reefs of Mauritius (Hayward, 1988) suggest that this species may be characteristic of biogenic rubble on an otherwise soft-sediment seafloor.

DISCUSSION

Bryorachis is a significant new addition to the family Phidoloporidae inasmuch as it has colonial and zooidal morphologies transitional between *Reteporellina* Harmer, 1933, a genus ranging from the shallow subtidal to shelf and slope depths, and *Chevron* Gordon, 1989, an unusual genus of small V-shaped colonies occurring on deep-sea oozes. *Reteporellina* comprises a number of species of erect, mostly open-branched

bryozoans, some fairly small. The colonies are characteristically fixed to a hard substratum. Among the characteristic features of the genus are the generally projecting subtubular peristome with an irregular rim and an open or closed pseudosinus, as well as the ovicell with conspicuous lateral processes and median labellum. The peristomial characters of *Bryorachis* accord well with those of *Reteporellina*, but not the ovicellular (or indeed colonial) ones. On the other hand, *Bryorachis* has a significant number of characters in common with *Chevron*. These include: similar peristomial features (i.e., either a pseudosinus or closed labial pore and suture) and primary orifice, a frontal granular-tubercular area, similar adventitious avicularia, and, in one of the two *Chevron* species, an identical ovicell. We would argue, based on morphological congruence and geographical distribution, that *Reteporellina* represents the most generalised taxon of the three considered here, with increasing specialisation shown by *Bryorachis* and *Chevron*. It would be useful to know precisely how colonies of the latter two genera are anchored to the substratum. Rootlets seem likely, but we have no evidence for these as yet.

The affinities of *Retelepralia* are not certain. In the absence of ovicells, Hayward (1988) included *Lepralia mosaica* in the genus *Hippopodina* (Hippopodiniidae). The absence of avicularia would be unusual in *Hippopodina*, which also has perforated ovicells, and, now that the ovicell is known, the combined characters seem more supportive of a relationship with the genera of Cheiloporinidae. These have a similar orifice and, typically, small or very reduced imperforate ovicells. On the other hand, the tubular connections and median frontal gymnocrystal strip in *Retelepralia* are hardly characteristic of the family so the question of affinity remains open.

ACKNOWLEDGEMENTS

We thank Mary Spencer Jones, The Natural History Museum, London, for a loan of Mauritian material of *Retelepralia mosaica*, and Bob Riel and Heather Winsor of the Electron Microscope Unit, James Cook University, for help to P.A. with SEM photography. Collection of Australian material was partly funded by Marine Science & Technology Research grants to Professor Michel Pichon (Université de Perpignan) and Alastair Birtles (James Cook University). DPG's research was carried out as part of NIWA's Marine Taxonomy Programme, funded by the N.Z. Foundation for Research, Science & Technology (Contract CO 1421).

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ASSESSMENT OF HORSEBACK SURVEYS OF KANGAROOS. *Memoirs of the Queensland Museum* 42(2): 504. 1998: Ground surveys of kangaroos form the basis of many studies on kangaroo habitat use, population dynamics and social organisation. They provide estimates of population composition and size, and the latter can be used to calibrate aerial counts. Walked line transects have been shown by Southwell (1994) to return accurate estimates of population size. Less time-consuming surveys using vehicles along tracks are frequently biased and not always possible, but may, nevertheless, provide useful indices of kangaroo numbers. An alternative is to conduct surveys on horseback.

Line transect methodology involves determining the distances to objects from the transect line. The decay in sightability away from the line is then modelled, allowing an estimate of density to be calculated. In order of importance, the technique carries four assumptions (Buckland et al., 1993):

- 1, Animals on the transect line are always seen
- 2, Animals do not move before being counted, and none are counted twice
- 3, Distances and angles are measured without error
- 4, Sightings are independent events.

Compared with foot surveys, horseback surveys may be more likely to meet these assumptions because kangaroos may flush later and not as far, and the observer can concentrate more on sighting animals than on negotiating the transect.

During Sept. 1993, foot and horseback surveys were compared along identical transects at two sites in central-western Queensland: Idalia NP (24°53'S, 144°46'E) and Terrick Terrick, a neighbouring sheep grazing property. At both sites, vegetation ranges from grassland to acacia woodland, with some areas of dense regrowth and fallen timber. On each site, four transects, each 5 km long, were walked by a single observer navigating using a sighting compass. Transects on Idalia were walked twice to boost sample size. For each transect, the two survey methods (horseback and foot) were separated by 24h, the order varying. Distances to kangaroos were determined with a rangefinder and angles from the transect line to each animal determined using a sighting compass, allowing perpendicular distances to be calculated. For each kangaroo species, data were pooled across each site for analysis and were analysed using the computer program DISTANCE (Buckland et al., 1993) as described by Clancy et al. (1997).

The two survey methods returned similar estimates of density for the three common species counted (Red Kangaroos, *Macropus rufus*, Common Wallaroos, *M. robustus*, and Eastern Grey Kangaroos, *M. giganteus*) (Table 1). The disparity for wallaroos on Terrick Terrick may be the result of heaping at zero distance during the horseback surveys, resulting in an overly steep sightability curve and inflated density estimate. At such high densities, observer saturation and

TABLE 1. Density estimates (D) and associated sample sizes (n) for horseback and foot surveys at the two sites.

Site	Kangaroo species	Horseback		Foot	
		D	n	D	n
Idalia	Red	13.89	(143)	15.67	(104)
Idalia	Wallaroo	21.08	(116)	22.75	(111)
Terrick Terrick	Red	18.44	(84)	16.53	(68)
Terrick Terrick	Wallaroo	85.16	(371)	59.97	(202)
Terrick Terrick	Eastern Grey	7.81	(25)	8.59	(55)

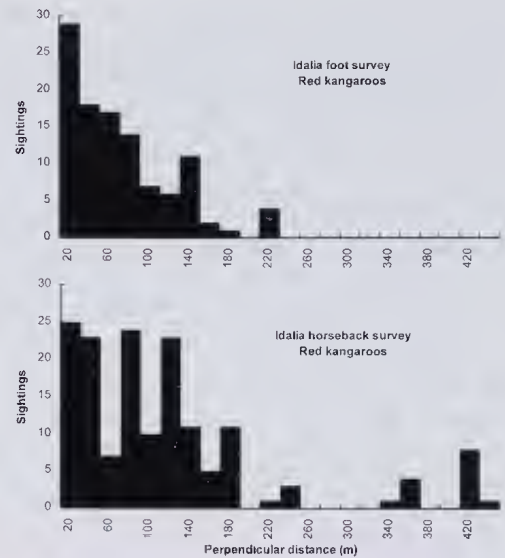


FIG. 1. Histograms of perpendicular distances of sightings of red kangaroos along transect lines conducted on foot and on horseback at Idalia NP.

reactive movement can also lead to inaccurate estimates (Southwell, 1994). Though not quantified, kangaroos appeared to flush later and not as far when confronted by an observer on horseback compared with one on foot. Horseback surveys generally yielded larger sample sizes (Table 1), which usually leads to improved modelling of sightability (Buckland et al., 1993). This larger sample size is reflected in much flatter sightability curves for horseback surveys compared with foot surveys (Fig. 1), presumably resulting from the higher vantage point. Surveying on horseback was approximately twice as fast as walking on foot and observers were less fatigued. Such advantages of horseback surveys must be contrasted with the additional costs of transporting and maintaining horses, and having observers competent with horses. Some habitats will be unsuitable for horseback surveys, such as steep terrain and thick vegetation, and fences create barriers, requiring access to gates.

Acknowledgements

We thank Glen Edwards and John Michelle for acting as observers on foot and horseback surveys, respectively. Comments from Stuart Cairns improved an earlier draft. This work was funded by Queensland Department of Environment.

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NEW SYNONYMS AND NOMENCLATURAL CHANGES IN THE ANT GENUS
POLYRHACHIS FR. SMITH (HYMENOPTERA: FORMICIDAE: FORMICINAE)

RUDOLF J. KOHOUT

Kohout, R.J. 1998 06 29: New synonyms and nomenclatural changes in the ant genus *Polyrhachis* Fr. Smith (Hymenoptera: Formicidae: Formicinae). *Memoirs of the Queensland Museum* 42(2): 505-531. Brisbane. ISSN 0079-8835.

Twenty-eight former subspecies are raised to species: *P. andromache semitestacea* Emery; *P. arcuata denselineata* Viehmeyer; *P. arcuspinosa waigeuensis* Donisthorpe; *P. atropos circumdata* Viehmeyer; *P. atropos tersa* Viehmeyer; *P. conops simpla* Santschi; *P. conops spinifera* Stitz; *P. continua procera* Emery; *P. costulata radiculicola* Dahl; *P. dahli cincta* Viehmeyer; *P. hipponianes hortensis* Forcl; *P. hipponianes lucidula* Emery; *P. labella obliqua* Stitz; *P. mayri obesior* Viehmeyer; *P. mucronata bismarckensis* Forel; *P. rastellata goraniensis* Emery; *P. relucens decipiens* Roger; *P. relucens litigiosa* Emery; *P. saevissima romanovi* Santschi; *P. santschii campbelli* Mann; *P. schang alata* Forel; *P. schang excitata* Viehmeyer; *P. schang leviuscula* Viehmeyer; *P. sexspinosa esuriens* Emery; *P. sumatrensis striatorugosa* Mayr; *P. textor aequalis* Forel; *P. thrinax javanica* Mayr and *P. villipes nocaensis* Forel. 47 synonyms of species-group names are proposed (senior names cited first): *P. andromache* Roger = *P. proxima semirufipes* Donisthorpe; *P. arcuata* (Le Guillou) = *P. arcuata continentis* Forcl; *P. aurita* Emery = *P. schlaginhaufeni* Viehmeyer = *P. schlaginhaufeni longispina* Viehmeyer; *P. batesi* Forel = *P. distincta* Karavaiev; *P. bicolor* Fr. Smith = *P. bicolor concolor* Forel; *P. caeciliae* Forel = *P. punctata* Karavaiev; *P. carbonaria* Fr. Smith = *P. orsyllus dentulata* Stitz = *P. orsyllus subcarinata* Emery; *P. caulomma* Viehmeyer = *P. caulomma parallela* Viehmeyer; *P. conops* Forel = *P. conops stitzi* Santschi; *P. continua* Emery = *P. continua revocata* Viehmeyer; *P. creusa* Emery = *P. creusa distinguenda* Karavaiev; *P. cyrus* Forel = *P. urania* Forel; *P. decipiens* Roger = *P. restituta* Viehmeyer = *P. restituta conclusa* Viehmeyer; *P. dives* Fr. Smith = *P. dives siwiensis* Santschi; *P. doddi* Donisthorpe = *P. townsvillei* Donisthorpe; *P. esuriens* Emery = *P. arcuspinosa* Donisthorpe = *P. juxtaspinosa* Donisthorpe; *P. goraniensis* Emery = *P. coronata* Santschi; *P. hermione* Emery = *P. daemeli sulciventris* Forel; *P. leviuscula* Viehmeyer = *P. schang laurae* Menozzi; *P. limbata* Emery = *P. verticalis* Santschi; *P. litigiosa* Emery = *P. sericata pruinosa* Santschi; *P. marginata* Fr. Smith = *P. rotundiceps* Karavaiev; *P. melpomene* Emery = *P. dolichocephala* Viehmeyer; *P. moesta* Emery = *P. paromalus tobias* Forel; *P. nigropilosa* Mayr = *P. nigropilosa conophthalma* Emery; *P. numeria* Fr. Smith = *P. schizospina* Karavaiev; *P. obtusa* Emery = *P. arcuata aruana* Karavaiev; *P. queenslandica* Emery = *P. dahli unisculpta* Viehmeyer; *P. radiculicola* Dahl = *P. karawaiewi* Santschi; *P. rixosa* Fr. Smith = *P. lycidas* Fr. Smith; *P. rufofemorata* Fr. Smith = *P. biroi* Forel = *P. biroi bidentata* Stitz = *P. biroi paprika* Forel; *P. sculpturata* Fr. Smith = *P. sumatrensis hamulata* Emery; *P. sericeopubescentis* Donisthorpe = *P. inusitata* Kohout; *P. solmsi* Emery = *P. alexandri* Karavaiev; *P. spinifera* Stitz = *P. continua hirsutula* Emery; *P. striata* Mayr = *P. striata assamensis* Forel; *P. striatorugosa* Mayr = *P. striatorugosa exophthalma* Forcl; *P. vestita* Fr. Smith = *P. vestita unicolor* Emery; *P. vigilans* Fr. Smith = *P. pyrgops* Viehmeyer and *P. villipes* Fr. Smith = *P. sumatrensis* Fr. Smith = *P. striata tritschleri* Forcl. *P. hoesi* Donisthorpe, formerly synonymised with *P. inermis* Fr. Smith, and *P. mentor* Forel, formerly synonymised with *P. limbata* Emery, are reinstated as valid species. *P. olybria* Forel, originally described from a queen and placed in the subgenus *Myrmhiopla* Forel, is recognised as a member of the nominal subgenus *Polyrhachis* and the identity of the worker caste established. Material of three unavailable names is referred to valid species (valid names cited first): *P. andromache* Roger for '*P. sericata pruinosa harmsi*' Karavaiev; *P. foreli* Kohout for '*P. relucens decipiens papuana*' Emery and *P. obliqua* Stitz for '*P. relucens litigiosa aloseana*' Forel. Types of *P. bihamata minor* Karavaiev, *P. hookeri* Lowne, *P. jurii* Karavaiev, *P. pallescens* Mayr and *P. ypsilon synacantha* Santschi, which were previously reported inaccessible or missing, presumed lost, have been located and their specific identity, including previously proposed synonymy, confirmed. *P. eudora* Fr. Smith and *P. latreillei* (Guérin-Méneville) are declared species inquirendae. Lectotypes are designated for *P. creusa distinguenda* Karavaiev and *P. hermione* Emery. □ *Hymenoptera*, *Formicidae*, *Polyrhachis*, *taxonomy*, *nomenclature*, *synonymy*.

Rudolf J. Kohout, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 7 June 1997.

During visits to European and British museums in 1990, partly funded by an Australian Entomological Society Research/Travel Grant (Kohout, 1991), I was able to study a number of *Polyrhachis* types, including some that were previously considered lost. These studies, with those of a later European survey in 1992, revealed a number of species-level synonyms. Some, relevant to the Australian fauna, have been discussed elsewhere (Kohout, 1994: 135). In 1994 I visited the Zoological Institute of the Ukrainian Academy of Sciences in Kiev in order to examine the little-known types of *Polyrhachis* species described by Karavaiev. Their subsequent comparison with types of species formerly described by Emery, Forel, Fr. Smith, Stitz and Viehmeyer helped to clarify their specific identity and to unravel their extensive synonyms.

The following nomenclatural changes were compiled too late for inclusion in the catalogues of Bolton (1995) or Dorow (1995). I extend sincere thanks to both these colleagues for making their then unpublished computer-based manuscripts available for this study.

The treatment of species is arranged alphabetically within relevant subgenera and/or species-groups, which generally follow the classification of Dorow (1995). Despite some criticism (Hung, 1967) the subgenera of *Polyrhachis* provide useful foci for sorting of species in this otherwise large and difficult genus (Kohout & Taylor, 1990: 510; Dorow, 1995: 7). Publication dates and the spelling of species epithets and author's names follow Bolton (1995).

The measurements (in mm) and indices follow those of Kohout (1990: 499): TL = Total length (the necessarily composite measurement of the entire ant); HL = Head length (the maximum measurable length of the head in perfect full face view, measured from the anterior-most point of the clypeal border or teeth, to the posterior-most point of the occipital margin); HW = Head width (width of the head in perfect full face view, measured immediately in front of the eyes); CI = Cephalic index ($HW \times 100/HL$); SL = Scape length (length of the antennal scape, excluding its condyle); SI = Scape index ($SL \times 100/HW$); PW = Pronotal width (width of the pronotal dorsum measured at the bases of the pronotal spines, or across the humeri in species without spines); MTL = Metathoracic tibial length (maximum measurable length of the tibia of the hind leg).

Where a holotype is described herein as 'unique', this infers that there was only a single specimen available for that species description.

Abbreviations for institutions (with the names of cooperating curators) are: ANIC = Australian National Insect Collection, Canberra, Australia (Drs R.W. Taylor, S.O. Shattuck); BMNH = Natural History Museum, London, U.K. (Barry Bolton); BPBM = Bernice P. Bishop Museum, Honolulu, Hawaii, USA (Dr G.M. Nishida); BSMP = Bureau of Science, Manila, Philippines; CAS = California Academy of Sciences, San Francisco, CA, USA; HNHM = Hungarian Natural History Museum, Budapest, Hungary (Dr J. Papp); DEIE = Deutsche Entomologische Institut, Eberswalde, Germany (Dr A. Taeger); IRSN = Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (Drs P. Grootaert, P. Dessart); IZAS = Institute of Zoology, Ukrainian Academy of Sciences, Kiev, Ukraine (Dr A.G. Radchenko); MCSN = Museo Civico di Storia Naturale 'Giacomo Doria', Genova, Italy (Drs R. Poggi, V. Raineri); MHNG = Muséum d'Histoire Naturelle, Geneva, Switzerland (Drs C. Besuchet, I. Löbl); MNHN = Muséum National d'Histoire Naturelle, Paris, France (Dr J. Casevitz Weulersse); MNHU = Museum für Naturkunde, Humboldt-Universität, Berlin, Germany (Dr F. Koch); NHMB = Naturhistorisches Museum, Basel, Switzerland (Dr M. Brancucci); NHMW = Naturhistorisches Museum, Wien, Austria (Drs M. Fischer, S. Schödl); NRMS = Naturhistoriska Riksmuseet, Stockholm, Sweden (Drs K.-J. Hedqvist, F. Ronquist); OXUM = University Museum, Oxford, UK (Dr C. O'Toole); QMBA = Queensland Museum, Brisbane, Australia (Drs G.B. Monteith, C.J. Burwell); RMNH = Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (Dr Ing. C. van Achterberg); SMF = Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (Dr J.-P. Kopelke, W.H.O. Dorow); UDSB = Università Degli Studi Di Bologna, Italy (Prof. Dr Maria M. Principi); USNM = US National Museum, Washington, DC, USA (Dr D.R. Smith); ZSSM = Zoologische Staatssammlung, München, Germany (Dr E. Diller).

SYSTEMATICS

Genus *Polyrhachis* Fr. Smith, 1857
Subgenus *Campomyrma* Wheeler, 1911
Polyrhachis creusa Emery, 1897

Polyrhachis creusa Emery, 1897: 577. Holotype worker. Type locality: New Guinea, Ighibirei (L. Loria), MCSN (examined).

Polyrhachis (Campomyrma) creusa distinguenda Karavaiev, 1927: 7, fig. 1. Syntype workers. Type locality: Indonesia, Ambon I. (W. Karavaiev #3007), IZAS, QMBA (examined). Syn. nov.

(For full synonymy citations see Kohout & Taylor, 1990: 514).

REMARKS. Karavaiev described *P. creusa distinguenda* from five workers 'sämtlich einzeln aber nahe von einander gesammelt'. The original series comprised specimens in two distinct size classes, but Karavaiev considered them conspecific, since he described them as 'major' and 'minor' workers of a single species. However, examination of four syntypes shows that the type series includes two distinct species. The 'major' workers of the *P. creusa distinguenda* syntype series (#3007) resemble the syntypes of *P. creusa chlorizans* Forel from Ralum, Bismarck Archipelago so closely that they appear to be part of the same series. Kohout & Taylor (1990: 514) synonymised *P. creusa chlorizans* with *P. creusa* Emery, and this synonymy is now confirmed. The 'minor' workers of the *P. creusa distinguenda* series (#2452) are, on the other hand, identical to voucher specimens (ANIC, QMBA) compared formerly by Taylor (1989: 25) with the holotype of *P. insularis* Emery. I consider them conspecific.

LECTOTYPE DESIGNATION. I have designated a 'major' worker specimen from the Karavaiev collection (IZAS) as the lectotype of *P. creusa distinguenda* and the other 'major' specimen (QMBA) as paralectotype. Both are in good condition. They bear identical sets of three labels, as follows: - Amboina, Karavaiev, 3007; - 3007.

Coll. Karavaiev; - Syntypus ♀ *Polyrhachis creusa distinguenda* Karaw. (red tag).

Subgenus *Myrmatopa* Forel, 1915

Polyrhachis alata Forel, 1904 stat. nov.

Polyrhachis gracilis r. *alata* Forel, 1904: 177. Syntype workers. Type locality: Indonesia, Sulawesi, Patuhuang (H. Fruhstorfer), MHNG (examined).

Polyrhachis gracilis Emery; Forel, 1909: 232. Junior synonym of *P. schang* Forel.

Polyrhachis schang var. *alata* Forel; Emery, 1925: 181.

REMARKS. Direct comparison of a *P. alata* syntype with the syntypes of *P. schang* Forel and *P. gracilis* Emery shows them to be closely related. The two latter taxa are undoubtedly conspecific, but the general appearance of the *P. alata* type sets it well apart. The *P. gracilis* syntypes are more-or-less uniformly brown, with only the mouth parts, pronotal collar, appendages, and apical portion of the gaster a shade lighter. The *P. alata* syntype is distinctly bicoloured — mostly light yellowish-brown, with the occiput, lateral and ventral portions of the head, antennae (except the apical funicular segments), lateral portions of mesosoma, front coxae, legs (except trochanters)

and most of the petiole and gaster diffusely blotched medium to dark reddish-brown. The masticatory margins of the mandibles, denticles of the truncated median portion of the anterior clypeal margin, frontal carinae, mesonotal and lateral propodeal margins and the petiolar spines are narrowly bordered with very dark brown. This conspicuous colour pattern is particularly distinct in recently collected specimens (Sulawesi Utara, Dumoga-Bone Nat. Park, nr Danau Mooat, 1100m, 1 viii 1985, N. Stork). Besides its colour, the *P. alata* type differs from the other relevant types in its larger size (HL 1.53-1.79 in *P. alata* versus HL 1.40-1.50 in *P. gracilis*), with higher and more acute lateral margins to its mesonotum, and longer, more slender petiolar spines.

Polyrhachis excitata Viehmeyer, 1913

stat. rev.

Polyrhachis excitata Viehmeyer, 1913: 147, fig. Holotype worker. Type locality: Indonesia, Sulawesi (in copal), MNHU (examined).

Polyrhachis schang var. *excitata* Viehmeyer; Viehmeyer, 1914: 48, fig. 8.

REMARKS. *P. excitata* stands closest to *P. ulysse* Forel and shares with that species distinct, posteriorly raised lateral margins to the mesonotum, and relatively long petiolar spines. However, the *P. excitata* type differs from *P. ulysse* specimens in a number of characters, including the strongly raised frontal carinae, the more convex and shorter propodeal dorsum, the less divergent petiolar spines, and rather dense sculpturation of the head, mesosoma and gaster. Sculpturing in *P. ulysse* is distinctly finer, notably on the head and over the anterior portion of the pronotal dorsum. The characters separating *P. excitata* from *P. schang* are even more pronounced. They include the lack of highly raised frontal carinae in *P. schang*, its generally finer sculpturation, lighter colour and distinctly smaller size. I consider that Viehmeyer's action in reducing *P. excitata* to a subspecies of *P. schang* was unjustified, and confidently return *P. excitata* to its original species rank.

Polyrhachis leviuscula Viehmeyer, 1916

stat. nov.

Polyrhachis (Myrmatopa) schang var. *leviuscula* Viehmeyer, 1916: 164. Syntype workers. Type locality: Singapore (H. Overbeck), MNHU (examined).

Polyrhachis (Myrmatopa) schang var. *laurae* Menozzi, 1926: 100. Syntype workers. Type locality: Singapore (C.F. Baker), UDSB, USNM, QMBA (examined). Syn. nov.

REMARKS. Comparison of the *P. schang levi-uscula* and *P. schang laurae* syntypes shows them to be taxonomically inseparable and undoubtedly conspecific. Additionally, comparison of *P. schang* Forel and the *P. leviuscula* types confirms their separate specific status.

Polyrhachis solmsi Emery, 1887

Polyrhachis solmsi Emery, 1887: 224 (footnote), pl. 3, fig 12. Syntype workers, queens, males. Type locality: Indonesia, Java, Buitenzorg (Conte Solms Laubach), MCSN (examined).

Polyrhachis alexandri Karavaiev, 1906: 375, fig. 1. Syntype queens. Type locality: Indonesia, Java, Buitenzorg (W. Karavaiev), IZAS (examined). Syn. nov.

REMARKS. I have been unable to locate either of Karavaiev's two syntype queens of *P. alexandri* at Kiev (IZAS) or in any other examined European collection. However, I did find two probably relevant queens in the Karavaiev collection. They bear identical labels reading 'Java, Buitenzorg, Karavaiev 1184'. They were placed together with *P. muelleri* Forel, though they could not represent queens of that species, since they do not belong to the subgenus *P. (Myrmhopla)*. They do, however compare well with available queens of subgenus *P. (Myrmatopa)*. These specimens are very similar, differing significantly only in colour. One of them is generally light reddish-brown, with the gastral and most other body segments narrowly bordered with dark brown. The other is generally darker. These specimens compare well with Karavaiev's figure of *P. alexandri* and I am confident that his fig. 1 actually depicts one of them. I consider, also, that Karavaiev's figs 2 and 3 portray the head of the same specimen, despite Karavaiev's claim that they depict lateral and frontal views of *P. muelleri*.

Following comparison of these queens with the original description and Karavaiev's additional notes (kindly translated by Wolfgang Dorow), I accept them as the missing syntype queens of *P. alexandri*. Moreover, their comparison with available *P. (Myrmatopa)* material in the Emery (MCSN), Forel (MHNG) and QMBA collections indicates their close similarity to *P. solmsi*. I consider *P. alexandri* to be synonymous with that species, as formally proposed above.

Subgenus Polyrhachis Fr. Smith, 1857

Polyrhachis bihamata (Drury, 1773)

Formica bihamata Drury, 1773: 73, pl. 38, figs 7, 8. Worker. Type locality: Island of Johanna near Madagascar (locality evidently in error - see Bolton, 1973: 352). Location of type unknown.

Polyrhachis (Polyrhachis) bihamata var. *perplexa* Santschi, 1925: 92. Syntype workers. Type locality: Laos, Muong Pek (Vitalis de Salvaza), NHMB (examined). Synonymy by Hung, 1970: 16.

Polyrhachis (Polyrhachis) bihamata var. *minor* Karavaiev, 1927: 12. Holotype worker. Type locality: Indonesia, Java, Tjampca nr Buitenzorg (= Bogor) (Karavaiev #2390), IZAS (examined). Junior homonym of *P. minor* Forel, 1886: 241. Synonymy by Hung, 1970: 16.

Polyrhachis (Polyrhachis) bihamata var. *tonsilis* Santschi, 1928: 133. Syntype workers. Type locality: Indonesia, Sumatra, Sibolangit, 1918 (J.B. Corporaal), NHMB (examined). Synonymy by Hung, 1970: 16.

REMARKS. Hung (1970: 19) was unable to access the type of *P. bihamata minor* and based his proposed synonymy of that form with *P. bihamata* solely on its short original description. I have compared the unique holotype of *P. bihamata minor* with the syntypes of *P. bihamata tonsilis* Santschi, *P. bihamata perplexa* Santschi and abundant material of *P. bihamata* itself, and accept the earlier decision of Hung, but with some reservations. I consider *P. bihamata perplexa* undoubtedly conspecific with *P. bihamata*, but both the other forms differ from *P. bihamata* in several regards. As a result, I am inclined to follow Santschi, who considered *P. bihamata tonsilis* to be a transitional form between *P. bihamata* and *P. bellicosa* Fr. Smith. Judging from the available specimens, I believe that the synonymy of *P. bihamata minor* with *P. bihamata tonsilis*, and elevation of the latter to specific status could be justified. However, following arduous search in numerous collections, the only other known specimen representative of the '*P. bihamata tonsilis*' morph is a topotypical individual (Sumatra, Sibolangit, 1919, J.A. Loerzing). I am hesitant therefore to accept any of the above nomenclatural changes pending a detailed study of additional material when it becomes available.

Polyrhachis olybria Forel, 1912

Polyrhachis olybrius Forel, 1912: 73. Syntype queens. Type locality: Indonesia, Sumatra, Indrapura (Tritschler), MHNG, QMBA (examined).

Polyrhachis olybrius Forel; Emery, 1925: 197. Combination in *P. (Myrmhopla)*.

Polyrhachis bellicosa Fr. Smith; Hung, 1970: 5 (in part).

REMARKS. In contrast to the vast majority of *Polyrhachis* species, where queens are very much like workers, queens of the nominal subgenus *Polyrhachis* are very different. On the fully developed, winged mesosoma the mesonotal spines are evidently not adaptive, and are not present.

The petiolar spines are greatly reduced. In workers the height of the petiole is equal to or even greater than the length of the head, with the tips of the spines distinctly hook-shaped. The petiolar spines in queens are short and simply pointed. As a result of their dissimilarity to conspecific workers, the queens of *P. olybria* were originally described not only as a separate species, but were also placed in a different subgenus.

Comparison of *P. olybria* syntypes with recently collected material containing worker-associated sexuals has shown that the *P. olybria* syntype queens are conspecific with workers traditionally identified as *P. bellicosa* Fr. Smith. Subsequent study of classical and modern material reveals that SE Asian populations of '*P. bellicosa*' contain two distinct species — *P. olybria* and *P. bellicosa*. The former is apparently endemic to SE Asia, and the latter undoubtedly a New Guinea-based element which has extended its range into Indonesia, the Philippines and Malaysia. *P. bellicosa* is consequently relatively rare towards the northern and western limits of its distribution, where *P. olybria* is rather common. These species are easily separated by a number of characters of which the most conspicuous is the colour of the first gastral segment. The gaster of *P. bellicosa* is always uniformly black or very dark reddish-brown, while that of *P. olybria* is bicoloured, with the first segment ranging from very light yellowish-brown to medium reddish-brown. The propodeal dorsum in *P. bellicosa* is weakly margined, with the margins terminating posteriorly as medially-directed, short transverse ridges. In contrast, the propodeal dorsum in *P. olybria* lacks any trace of margins, and the posterior angles are produced as short but distinct acute spines, which are contiguous at the base to form a 'V'. Ocelli are always present in *P. bellicosa*, though the laterals are sometimes obscure. In *P. olybria* ocelli are lacking, with their relative positions occasionally marked by shallow depressions in the cephalic sculpturation. The petiolar spines also appear generally to be shorter in *P. bellicosa* than in *P. olybria*, and, despite small overlap in their petiolar index values (PI 87-108 in *P. bellicosa* versus PI 107-127 in *P. olybria*), they clearly indicate specific distinctiveness. In over 50 measured *P. olybria* specimens, the lowest PI values (107-112) were obtained from Sumatra, where *P. bellicosa* is so far unknown, while *P. olybria* PI values from Borneo, where both species are sympatric, were consistently higher (PI 118-127).

To assist in establishing the specific identity of the worker caste of *P. olybria*, I have selected two worker specimens to complement the syntype queens. These were originally identified by Forel as *P. bellicosa*, but comparison with modern material confirms their identity as *P. olybria*. These workers and the syntype queens are undoubtedly part of a single original series collected by Tritschler at Indrapura, Sumatra.

Polyrhachis ypsilon Emery, 1887

Polyrhachis ypsilon Emery, 1887: 239. Syntype workers (lectotype designated by Hung, 1970: 19). Type locality: Singapore (L.M. D'Albertis), MCSN (examined).

Polyrhachis (*Polyrhachis*) *ypsilon* ab. *synacantha* Santschi, 1933: 2. Holotype worker. Type locality: Borneo, Kp. Makoendjoeng (Baritoe Riv.) (Prince Léopold), IRSN (examined). Synonymy by Hung, 1970: 19.

(For full synonymy citations see Hung, 1970: 19).

REMARKS. When Hung proposed the above synonymy he was unable to locate the type of *P. ypsilon synacantha*, but was satisfied to consider this form an 'individual variant of the Borneo population' of *P. ypsilon*. This opinion was evidently based on Hung's understanding of Santschi's original description, which he translated to read 'petiolar spines are all parallel for some distance' and added that 'there are not any other significant deviations from the syntype worker of *P. ypsilon* and other specimens'.

I have examined the unique holotype of *P. ypsilon synacantha* in the collection of Prince Léopold (IRSN) and found it to be very unusual and undoubtedly an anomalous specimen. I believe that Hung's opinion in considering it a synonym of *P. ypsilon* was correct. However, his interpretation of the Santschi's description was inaccurate. The petiole of *P. ypsilon synacantha* is very peculiar, with the node rising as a huge, pillar-like structure, which terminates dorsolaterally as rather asymmetrical dentiform angles, with the apex furnished with two minute, uneven, posteriorly directed, acute spines.

Subgenus *Myrmothrinax* Forel, 1915

Polyrhachis aequalis Forel, 1910 stat. nov.

Polyrhachis textor var. *aequalis* Forel, 1910: 129. Syntype workers, queen. Original localities: Philippines, Luzon, Province of Zambales, Olongapo (C.S. Banks); Negros, Maa (C.S. Banks), BSMP (types destroyed - see Baltazar, 1966: 284), MHNG, QMBA (examined).

REMARKS. Examination of the *P. textor aequalis* syntypes and their comparison with the

holotype of *P. textor* Fr. Smith clearly shows these taxa to be distinct and separate species. The most obvious characters separating these taxa are their relative size (HL 1.50-1.56 in *P. aequalis* versus HL 2.09 in *P. textor*) and the configuration of their petiolar spines. In *P. textor* the median spine is at least twice as long as the lateral spines, while in *P. aequalis*, as the name suggests, all three spines are of equal length.

***Polyrhachis cincta* Viehmeyer, 1913 stat. nov.**

Polyrhachis dahli var. *cincta* Viehmeyer, 1913: 149. Syntype workers. Type locality: Indonesia, Sulawesi (in copal), MNHU (examined).

REMARKS. Comparison of the types of *P. dahlii* Forel, *P. dahli cincta* Viehmeyer, *P. dahli unisculpta* Viehmeyer and *P. queenslandica* Emery shows all to be closely related. However, while the last two are undoubtedly conspecific (see below under *P. queenslandica*), *P. dahlii* and *P. dahli cincta* appear to be distinct, valid species. The most apparent difference separating them is the characteristic honey-yellow colour of *P. dahlii*, versus the generally very dark reddish-brown colour of *P. dahli cincta*, with only the gaster and appendages a shade lighter. Moreover, in *P. dahlii* the frontal carinae are only slightly elevated (a little more-so than in *P. queenslandica*), while in *P. dahli cincta* they are distinctly raised. In profile the mesonotal dorsum in *P. dahlii* is only marginally higher than the propodeum, while in *P. dahli cincta* the metanotal groove is accentuated by a distinct step-like transition between the mesonotum and propodeum. Also, the dorsum of the mesosoma in *P. dahlii* is densely punctate, without any apparent pattern of orientation, while the mesosomal sculpturation in *P. dahli cincta* is more-or-less distinctly longitudinally punctate-striate. I therefore confidently designate *P. cincta* as a species separate from *P. dahlii*.

***Polyrhachis javanica* Mayr, 1867 stat. nov.**

Polyrhachis thrinax var. *javanica* Mayr, 1867: 52. Holotype worker. Type locality: Indonesia, Java, [Mus. Holm = ?Holmgren] (location of type unknown).

REMARKS. The holotype of *P. thrinax javanica* cannot be found in the NHMW collection and must be presumed lost. Mayr, however, gave a description sufficient to allow reasonably confident identification of *P. javanica*. It clearly shows *P. javanica* to be a species separate from *P. thrinax* Roger.

***Polyrhachis queenslandica* Emery, 1895**

Polyrhachis queenslandica Emery, 1895: 356. Syntype workers. Type locality: Australia, Qld, Kamcrunga (M. Podenzana), MCSN, MHNG (examined).

Polyrhachis dahli var. *unisculpta* Viehmeyer, 1914: 48. Syntype workers, queen. Type locality: New Guinea, Wareo, MNHU (examined). Syn. nov.

REMARKS. Comparison of the *P. queenslandica* and *P. dahli unisculpta* syntypes shows them to be taxonomically inseparable, evidently representing Australian and New Guinean populations of a single species.

Subgenus *Chariomyrma* Forel, 1915
***Polyrhachis arcuata* (Le Guillou, 1842)**

Formica arcuata Le Guillou, 1842: 315. Syntype queen, worker. Type locality: Borneo (for queen), N Australia (for worker), MNHN (types presumed lost).

Polyrhachis latifrons Roger, 1863: 155. Syntype workers. Type locality: Indonesia, Bintang I., MNHU (examined). Synonymy with *P. modiglianii* by Emery, 1895: 357; with *P. arcuata* by Emery, 1897: 583.

Polyrhachis arcuata (Le Guillou); Mayr, 1863: 443. Combination in *Polyrhachis*.

Polyrhachis modiglianii Emery, 1888: 529, pl. 9, fig. 1. Syntype workers. Type locality: Indonesia, Sumatra, Padang (E. Modigliani), MCSN (examined). Synonymy with *P. latifrons* Roger by Emery, 1895: 357.

Polyrhachis arcuata var. *continentis* Forel, 1905: 179. Syntype workers. Type locality: W Malaysia (Malacca, Pahang), MHNG (examined). Syn. nov.

REMARKS. The types of *P. arcuata* cannot be found in the MNHN or any other European collection and must be considered lost. However, the examination of the syntypes of *P. latifrons* Roger and *P. modiglianii* Emery, both of which were previously synonymised with *P. arcuata*, shows the *P. arcuata continentis* syntypes to be conspecific with them. The putative distinguishing characters given in the original *P. arcuata continentis* description are insignificant when the types are compared with specimens from a more extensive distributional range. I conclude that there is no justification for *P. arcuata continentis* to be recognised as a taxon separate from *P. arcuata*.

***Polyrhachis aurita* Emery, 1911**

Polyrhachis aurita Emery, 1911: 538. Syntype workers. Type locality: New Guinea, Cyclops Mts, MCSN (examined).

Polyrhachis schlaginhaufeni Viehmeyer, 1912: 12. Syntype workers. Type locality: New Guinea, Tor-

ricelli Mts (O. Schlaginhaufen), MNHU (examined). Syn. nov.

Polyrhachis schlaginhaufeni var. *longispina* Viehmeier, 1912: 12. Syntype workers. Type locality: New Guinea (O. Schlaginhaufen), MNHU. Syn. nov.

REMARKS. I have directly compared syntypes of *P. aurita* and *P. schlaginhaufeni* and I am confident that they are conspecific. They were originally distinguished only by minor differences in the length and direction of spines. Such features are known to be of no value in differentiating species in this subgenus. I have been unable to locate either of the two *P. schlaginhaufeni longispina* syntypes. However, their original description clearly states that the only differences between them and *P. schlaginhaufeni* are the thickness and direction of the propodeal spines and their exceptional length (as the name *longispina* implied). I have examined a single specimen (in the QMBA collection) which fits the *P. schlaginhaufeni longispina* description, and am satisfied that this form is conspecific with *P. aurita*.

Polyrhachis caulomma Viehmeier, 1914

Polyrhachis caulomma Viehmeier, 1914: 57, fig. 12. Holotype worker. Type locality: New Guinea, Wareo, MNHU (examined).

Polyrhachis caulomma var. *parallela* Viehmeier, 1914: 612. Holotype worker. Type locality: New Guinea, Wareo, MNHU (examined). Syn. nov.

REMARKS. Direct comparison of the types of *P. caulomma* and *P. caulomma parallela* clearly demonstrates that the separate status of these forms was originally based on trivial characters, such as the length and direction of the propodeal spines. Considering the great variability in these structures in *Polyrhachis* workers, notably in subgenus *P. (Chariomyrma)*, I propose the above synonymy.

Polyrhachis cyrus Forel, 1901

Polyrhachis cyrus Forel, 1901: 32. Syntype workers, queens, males. Type locality: Bismarck Archipelago, Ralum (PNG, East New Britain Prov.) (F. Dahl), MHNG, MNHU, QMBA (examined).

Polyrhachis urania Forel, 1902: 516. Syntype workers. Type locality: Australia, Qld, Mackay (G. Turner), MHNG (examined). Syn. nov.

REMARKS. I have directly compared the types of *P. cyrus* and *P. urania* and find them remarkably similar. The most obvious difference between them is the density of the cephalic pubescence, which is almost completely lacking in *P. cyrus*, but rather dense in *P. urania*, where

it completely obscures the underlying sculpturation. Also, the propodeal spines in *P. cyrus* are slender and almost straight, while in *P. urania* they are broad and sinuate, with their tips turned distinctly outwards. However, when specimens from the whole range of distribution are examined, these characters seem to integrate, notably in a short series of specimens from Papua New Guinea (PNG), Central Prov. (Port Moresby-Brown River Rd, 20 i 1968, B.B. Lowery) which are intermediate between the two named forms.

In the original description of *P. urania* Forel noted that: 'Cette forme n'est peut-être qu'une race australienne de la *P. Cyrus* de l'Archipel de Bismarck'. I consider this opinion to be correct, and that these forms are taxonomically inseparable, with '*P. urania*' representing an Australian population of its new senior synonym, *P. cyrus*.

Polyrhachis denselineata Viehmeier, 1914 stat. nov.

Polyrhachis arcuata var. *denselineata* Viehmeier, 1914: 533. Syntype workers. Type locality: New Guinea, Rawlinsongebirge, MNHU (examined).

REMARKS. In lieu of the missing types of *P. arcuata* (see above under that species) I have compared a syntype of *P. arcuata denselineata* with the syntypes of *P. latifrons* Roger and *P. modigliani* Emery, both formerly synonymised with *P. arcuata* by Emery (1895: 357 and 1897: 583). I find *P. denselineata* to be a distinct species. The dorsa of the head, mesosoma and gaster are finely longitudinally striate, and the pronotal shoulders produced as distinct teeth. In comparison, the pronotal shoulders in *P. arcuata* are obtuse, while the longitudinal body striation is more coarse and irregular. This sculpturing is limited to the dorsa of the head and mesosoma, with the gaster finely shagreened. The petiolar dorsum of *P. arcuata denselineata* has a prominent, spine-like, intercalary tooth which is rather obscure or totally absent in *P. arcuata*. In addition, the rich, relatively long, hair-like pilosity of *P. latifrons* and *P. modigliani* is greatly reduced in *P. arcuata denselineata* and confined mostly to the head and gaster, with only a few hairs present on the mesosomal dorsum. The characters differentiating these taxa appear to be consistent in available material and I am confident in considering *P. denselineata* a species separate from *P. arcuata*.

Polyrhachis hookeri Lowne, 1865

Polyrhachis hookeri Lowne, 1865: 334. Syntype workers. Type locality: Australia, New South Wales,

vicinity of Sydney (B.T. Lowne), ?BMNH (types presumed lost), NHMW (examined).

(For full synonymy citations see Kohout, 1994: 136).

REMARKS. Kohout & Taylor (1990: 515) believed the type/s of this species to be lost. However, during my most recent visit to the Mayr collection in Vienna, I found a single specimen of *P. hookeri* which undoubtedly represents a part of the Lowne's original series. This is surely the specimen referred to by Mayr (1876: 73) as '... ein ♂ in meiner Sammlung von Herrn Lowne' and have labelled it as a syntype of *P. hookeri*. Subsequent study has confirmed the identity of the previously selected voucher specimen ('paradigm') of *P. hookeri* discussed by Kohout & Taylor (1990: 515), and supports the synonymy of *P. cataulacoidea* Stitz proposed by Kohout (1994: 136).

Polyrhachis limbata Emery, 1897

Polyrhachis limbata Emery, 1897: 585, pl. 1, fig. 24. Holotype worker. Type locality: New Guinea, Sorong (L.M. D'Albertis), MCSN (examined).

Polyrhachis (Chariomyrma) abrupta Karavaiev, 1927: 19, fig. 10. Syntype workers. Indonesia, Aru Is, Wammar I. (W. Karavaiev #2586?, 3001), IZAS, QMBA (examined). Junior primary homonym of *Polyrhachis abrupta* Mayr, 1867.

Polyrhachis verticalis Santschi, 1928: 139. Replacement name. Syn. nov.

(*Polyrhachis mentor* Forel; Viehmeyer, 1914: 54.) Spurious synonymy.

REMARKS. I have directly compared the types of *P. limbata*, *P. verticalis* and *P. mentor* (MNHU) and am confident that *P. limbata* and *P. verticalis* represent a single species. The unique holotype of *P. limbata* appears somewhat worn, having lost most of the characteristic reddish pubescence, which is still evident in the syntypes of *P. verticalis* (and very conspicuous in modern specimens). Otherwise these types are closely comparable. However, I disagree with the synonymy of *P. mentor* with *P. limbata* as proposed by Viehmeyer (1914: 54). These species are superficially similar, mainly because of their shared reddish pubescence, but they are structurally well-differentiated. *P. mentor* is distinctly more slender, notably towards the propodeal dorsum, which is distinctly narrower than in specimens of *P. limbata*. The anterior margin of the petiolar dorsum is narrowly rounded, with almost straight, posteriorly diverging spines. The head and pronotal dorsum are finely, fairly regularly striate, while underlying reddish pubescence is almost lacking on the head and much diluted elsewhere, except on the gaster. In comparison, *P. limbata* is distinctly more robust, with sculpturation more-or-less striate-

rugose, and underlying reddish pubescence rather dense, notably on the mesosomal dorsum and gaster. The anterior margin of the petiolar dorsum is broadly rounded, and relatively long semicircular spines embrace the first gastral segment.

P. limbata is known to range from the Indonesian Aru Is to the New Guinean mainland, where it was most recently recorded from Torricelli Mts (West Sepik Prov., Lumi, 400-550m, 03° 28'S, 142°02'E, 4-13 viii 1984, R.J. Kohout acc. 84.262). *P. mentor* appears to be restricted to islands of the Bismarck Archipelago where the unique holotype was collected by F. Dahl on the 'wooded summit of Wunakokur' (= Vunakokor [Mt Varzin], c. 20km S of Rabaul, New Britain). The only other specimen I have seen was collected on New Ireland (Lelet Plateau, 800-1000m, c. 03°20'S, 151°56'E, 19-24 vii 1984, R.J. Kohout acc. 84.95).

It could be argued that, considering their superficial likeness and disjunct distributional ranges, *P. mentor* might represent an isolated population conspecific with *P. limbata*. However, in view of the scarcity of study material this assumption is purely hypothetical. I believe that the differences outlined above are sufficient to justify the separate specific status of these forms.

Polyrhachis marginata Fr. Smith, 1859

Polyrhachis marginatus Fr. Smith, 1859: 139. Holotype worker. Type locality: Indonesia, Aru Is (A.R. Wallace), OXUM (examined).

Polyrhachis (Chariomyrma) rotundiceps Karavaiev, 1927: 18. Syntype workers. Type locality: Indonesia, Aru Is, Wammar I. (W. Karavaiev #2570, 3003), IZAS, QMBA (examined). Syn. nov.

REMARKS. Karavaiev was evidently unaware of Smith's *P. marginata*. Comparison of its type with those of *P. rotundiceps* shows them to be synonyms.

Polyrhachis obtusa Emery, 1897

Polyrhachis aurea var. *obtusa* Emery, 1897: 589. Syntype workers. Original localities: New Guinea, Haveri, Kapa Kapa, Humboldt Bay (L. Loria), MCSN, MNHG, QMBA (examined).

Polyrhachis obtusa Emery; Kohout & Taylor, 1990: 516. Raised to species.

Polyrhachis arcuata var. *aruana* Karavaiev, 1927: 16. Syntype workers. Indonesia, Aru Is, Wammar I. (W. Karavaiev #2531, 2644, 3002) IZAS, QMBA (examined). Syn. nov.

REMARKS. Direct comparison of the syntypes of *P. obtusa* and *P. arcuata aruana*, together with more recent material from Indonesia and PNG,

demonstrates that these names have been applied to a single biological species.

***Polyrhachis pallescens* Mayr, 1876**

Polyrhachis guerini var. *pallescens* Mayr, 1876: 74. Holotype worker. Type locality: Australia, Qld, Rockhampton (A. Dietrich), NHMW (examined). *Polyrhachis pallescens* Mayr; Kohout & Taylor, 1990: 516. Raised to species. (Full synonymy citations see Kohout & Taylor, 1990: 516).

REMARKS. Kohout & Taylor (1990: 516) raised *P. pallescens* to specific rank and considered *P. aurea depilis* Emery to be its junior synonym. At that time the holotype of *P. pallescens* could not be located and the possibility of its destruction was accepted. It was suggested that all the unique types of species described by Mayr from the material of various museums, including the Godeffroy, were returned to their original owners. Following the collapse of the firma Godeffroy, almost its entire collection was transferred to Hamburg Museum, and mostly destroyed during World War II. However, I have located in the Mayr collection a number of *Polyrhachis* specimens, most of them bearing original Godeffroy Museum labels, pinned as a separate group. Most of these are type specimens of *Polyrhachis* species described by Mayr (1876) from Godeffroy Museum material. They include the type of *P. pallescens*. It is well-documented that Mayr did not label specimens used for his descriptions to indicate their status, and this perhaps explains why these types have remained undetected for so long. Following examination of its unique holotype, the separate specific status of *P. pallescens* versus *P. guerini*, and the junior synonymy of *P. aurea depilis*, as proposed by Kohout & Taylor (1990: 516), are confirmed.

***Polyrhachis radicolica* Dahl, 1901 stat. nov.**

Polyrhachis costulata var. *radicolica* Dahl, 1901: 15. Workers, queens (alate), males. Type locality: Bismarck Archipelago, Ralum (F. Dahl) MHNG, MNHU, QMBA (specimens from the original series examined). [First available use of *Polyrhachis aurea* r. *costulata* var. *radicolica* Forel, 1901: 32 (unavailable infrasubspecies)].

Polyrhachis (Chariomyrma) convexa Karavaiev, 1927: 17, fig. 7b. Syntype workers. Type locality: Indonesia, Ambon I., Hito (W. Karavaiev #2976) IZAS, QMBA (examined). Junior primary homonym of *Polyrhachis convexa* Roger, 1863.

Polyrhachis (Chariomyrma) karawaiewi Santschi, 1928: 139. Replacement name. Syn. nov.

REMARKS. Comparison of a *P. karawaiewi* syntype with specimens from the original series of *P.*

costulata radicolica shows them to be conspecific.

P. nigrescens is a species very similar to *P. karawaiewi*. It was described by Karavaiev (1927: 16) in the same paper as his junior homonym '*P. convexa*', which was later replaced by Santschi's *P. karawaiewi*. The most obvious differences between these taxa are their relative size and the outline of the mesosomal dorsum in lateral view. *P. karawaiewi* is consistently smaller, with a highly convex mesosomal dorsum, while the larger *P. nigrescens* has the mesosomal dorsum only slightly arched. This character is especially conspicuous when specimens of both species are directly compared. However, I have seen material from Jilolo District (Halmahera, Indonesia) and Kavieng (New Ireland Prov., PNG) in which specimens matching both nominal species are mounted on the same pin. I have also collected a series at Baderi village (Northern Province, PNG) which ranges in character between these forms, with the smallest specimens very closely matching the type of *P. karawaiewi*, and the larger specimens closely similar to the *P. nigrescens* type. Similar variability is seen in specimens from several other PNG series. It is clearly possible that these nominal species represent a single, albeit variable, species. Unfortunately the head of the single *P. nigrescens* syntype available for this study is missing and I am reluctant to propose synonymy of these nominal taxa until other specimens in good condition become available.

Subgenus *Hedomyrma* Forel, 1915

***Polyrhachis campbelli* Mann, 1919 stat. nov.**

Polyrhachis (Hedomyrma) santschii subsp. *campbelli* Mann, 1919: 376. Syntype workers. Type locality: Solomon Is, Russell I., West Bay, 1916 (W.M. Mann), MCZC (Type 9192) (examined).

REMARKS. Comparison of the holotype of *P. santschii* Mann with syntypes of *P. santschii campbelli* clearly shows they represent separate species. The pronotal spines are rather short and broad at their bases in *P. campbelli*, while in *P. santschii* the spines are slender, much longer, and distinctly curved downwards. The propodeal spines in *P. santschii* are also very prominent, more-or-less horizontal, and with a distinctly broader, longitudinally striate base. Generally silver or pale-golden pubescence is well developed over most of the body in *P. campbelli*, while it is almost absent in *P. santschii*, except on the gastral dorsum, where it has a relatively more distinctly golden hue.

***Polyrhachis circumdata* Viehmeyer, 1913**
stat. rev.

Polyrhachis circumdata Viehmeyer, 1913: 152, fig. Syntype workers, queen. Type locality: Indonesia, Sulawesi (in copal), MNHU (workers examined).

Polyrhachis atropos var. *circumdata* Viehmeyer, 1914: 52. Reduced in rank to variety of *P. atropos* Fr. Smith.

REMARKS. Comparison of the *P. atropos* holotype with *P. circumdata* syntypes demonstrates that Viehmeyer's (1914) action in reducing the rank of the latter cannot be justified. These taxa are very distinct, notably in the form of the pronotal dorsum, which is relatively large in *P. atropos*, appearing somewhat disproportionate to the rest of the body, with its spines rather broad and the lateral borders only weakly emarginate at their bases. In *P. circumdata* the pronotal dorsum is distinctly more narrow, with its sides deeply emarginate at the bases of the relatively slender spines. I am confident that these forms represent separate species.

***Polyrhachis hermione* Emery, 1895**

Polyrhachis hermione Emery, 1895: 357. Syntype workers. Type locality: Australia, Qld, Mt Bellenden Ker (M. Podenzana), MCSN, MHNG (examined).

Polyrhachis daemeli var. *sulcativentris* Forel, 1915: 111. Syntype workers. Type locality: Australia, Qld, MHNG (examined). Syn. nov.

Polyrhachis daemeli var. *sulcativentris* Emery, in Forel; Bolton, 1995: 357.

Polyrhachis daemeli sulcativentris Mayr; Dorow, 1995: 27.

REMARKS. Despite extensive search in the Forel (MHNG) and Emery (MCSN) collections I have not located the type of *P. daemeli sulcativentris*. However, examination of a *P. hermione* syntype in the Emery collection revealed that it bears a handwritten tag reading '*Polyrhachis sculptiventris* Emery', with the name '*sculptiventris*' crossed-out and replaced by the name '*Hermione*'. Similarly, a syntype of *P. hermione* in the Forel collection, which Emery had apparently sent to Forel before the description of *P. hermione* was published, bears a name tag '*Polyrhachis Dämeli* var. *sculptiventris* n. var. Queensland'. This specimen agrees entirely with the short description of *P. daemeli sulcativentris*, and undoubtedly represents the original specimen to which Forel (1915: 110) referred when he described *P. daemeli exlex*. From Forel's statement it is obvious that he had intended only to point out the similarity of his new species and Emery's '*sculptiventris*', the description of which he thought had already been published. Forel was

evidently unaware of Emery's earlier decision to change that species name before publication from *P. sculptiventris* to *P. hermione*, and clearly misread the handwritten name '*sculptiventris*' on the label of his *P. hermione* specimen as '*sulcativentris*', thus erroneously establishing the name *P. daemeli sulcativentris*, which can now be laid to rest.

LECTOTYPE SELECTION. To establish the identity of both relevant names I have selected the Emery collection syntype as the lectotype of *P. hermione* Emery. It is mounted on its left side on a card, and has the right foreleg and both hind legs missing and the right propodeal spine broken off. It is otherwise in relatively good condition. In addition to the name tag discussed above, it bears the following three labels: a tag in Emery's handwriting reading 'Mt Bellendenker Queensland', 'TYPUS' (in red print), and a yellow tag 'Collezione EMERY'. The syntype in the Forel collection, which is clearly a part of the same series, is mounted on an identical stage card in the same manner, but on its right side. In addition to the original name-tag in Emery's handwriting (see above), it bears a small blue tag reading 'Cotyus' and three additional labels, each in a different handwriting, reading: 'G. *Polyrhachis* Sm', 'S.G. *Hedomyrma* For.' and 'Sp. *Daemeli* Mayr'. This specimen is recognised here as a paralectotype of *P. hermione*. Also, as a result of Forel's (1915) action, I deem both these specimens to be syntypes of *P. daemeli sulcativentris* Forel and have labelled them accordingly.

***Polyrhachis melpomene* Emery, 1897**

Polyrhachis melpomene Emery, 1897: 592. Syntype workers, queen. Type locality: New Guinea. Haveri (L. Loria), MCSN (examined).

Polyrhachis dolichocephala Viehmeyer, 1914: 532, fig. 5. Holotype worker. Type locality: New Guinea, Rawlinsongebirge, MNHU (examined). Syn. nov.

REMARKS. Direct comparison of types of both relevant names shows this to be a straightforward synonymy. Viehmeyer was very likely unaware of Emery's *P. melpomene*, since in the original description of *P. dolichocephala* he compares that taxon with *P. fervens* Fr. Smith rather than *P. melpomene*.

***Polyrhachis tersa* Viehmeyer, 1914 stat. nov.**

Polyrhachis atropos var. *tersa* Viehmeyer, 1914: 52. Holotype worker. Type locality: New Guinea, Sattelberg, MNHU (examined).

REMARKS. Examination of the holotypes of *P. atropos* Fr. Smith and *P. atropos tersa*, shown them to be taxonomically distinct, undoubtedly

representing separate species. The pronotal dorsum of *P. atropos tersa* is more like that of *P. circumdata* (see above). However, in that species the pronotum is widest near the pro-mesonotal suture, while in *P. tersa* the lateral pronotal margins are more rounded with the pronotal dorsum widest in the middle. Also, the mesosomal dorsum in *P. tersa* appears more slender than that of *P. circumdata*, with the sides of the mesonotum strongly convergent posteriorly and the propodeal dorsum distinctly narrower, notably across the propodeal suture. The longitudinal striation of the mesonotal and propodeal dorsa in *P. circumdata* is much less coarse than that on the pronotum, but still apparent, whereas the mesonotal and propodeal dorsa in *P. tersa* are only weakly micro-reticulate and almost smooth. In addition, the head and antennal scapes in *P. tersa* are somewhat longer, with CI 79-83 and SI 158-162, versus CI 86-87 and SI 147 in the three *P. circumdata* syntypes.

Subgenus *Myrmhopla* Forel, 1915

Polyrhachis bicolor species-group

Polyrhachis bicolor Fr. Smith, 1858

Polyrhachis bicolor Fr. Smith, 1858. Holotype queen.

Type locality: Burma, BMNH (examined).

Polyrhachis bicolor var. *concolor* Forel, 1910: 129. Syntype workers, queen, male. Type locality: Philippines, Luzon, Manila (C.S. Banks), BSMP (types destroyed - see Baltazar, 1966: 282), MHNG (examined). Syn. nov.

REMARKS. *P. bicolor* was first reported from Australia (Northern Territory, Darwin) by Clark (1941: 69) and subsequently included by Kohout & Taylor (1990: 511) in their list of Australian *Polyrhachis* species. The identification of Clark's specimens has, however, never been verified. Recent collecting (by A.N. Andersen, H. Reichel, R.J. Kohout) has provided abundant additional material, including several queens. Their comparison with the holotype queen of *P. bicolor* (BMNH) finally establishes that the Australian specimens are conspecific with that species. Subsequent study of several infraspecific forms of *P. bicolor* in the Forel collection (MHNG) demonstrates that the characters used by Forel to separate *P. bicolor concolor* and *P. bicolor* are trivial. I consider them as representatives of a single species.

In the course of this study I have also examined those infraspecific taxa of the *P. bicolor*-complex described by Karavaiev; namely *P. bicolor atrocastanea*, *P. bicolor aurata*, *P. bicolor erecta* and *P. bicolor weyeri*. I consider that most, if not all, represent valid species. However, the *P. bicolor*

species-group, as delimited by Dorow (1995: 49), contains a number of other unresolved taxa and their treatment is beyond the scope of this study. Resolution of the complex will require detailed examination of all specific and infraspecific named entities, types of which are not presently available. Their taxonomy will therefore be dealt with separately.

Polyrhachis dives species-group

Polyrhachis dives Fr. Smith, 1857

Polyrhachis dives Fr. Smith, 1857: 64. Holotype worker. Type locality: Singapore (A.R. Wallace). BMNH (examined).

Polyrhachis (Myrmhopla) dives var. *siwiensis* Santschi, 1932: 20. Holotype queen. Type locality: New Guinea. Siwi (Forêt) (Prince Léopold), IRSN (examined). Syn. nov.

(For full synonymy citations see Bolton, 1995: 347 and Dorow, 1995: 52.)

REMARKS. I have compared the holotype queen of *P. dives siwiensis* with numerous *P. dives* queens from a wide distributional range, and believe that the characters given by Santschi do not justify the separate status of the former as a subspecies of *P. dives*. The slightly larger head and the rather short propodeal spines sets the queen of *P. dives siwiensis* somewhat apart, but these differences seem to be taxonomically insignificant. In fact, the holotype compares relatively well with a somewhat aberrant queen collected in N Qld in a nest of 'normal' *P. dives* workers. I am therefore confident in considering the holotype queen of *P. dives siwiensis* to be a variant individual, and consequently a synonym of *P. dives*.

Polyrhachis mucronata species-group

Polyrhachis batesi Forel, 1911

Polyrhachis batesi Forel, 1911: 301. Holotype worker.

Type locality: Indonesia, Seram I. (Bates), ZSSM (examined).

Polyrhachis (Myrmhopla) distincta Karavaiev, 1927: 40, fig. 18. Syntype workers. Type locality: Indonesia, Ambon I. (W. Karavaiev), IZAS, QMBA (examined). Syn. nov.

REMARKS. This is a straightforward synonymy. Karavaiev was evidently unaware of Forel's prior available species name.

Polyrhachis bismarckensis Forel, 1901

stat. nov.

Polyrhachis mucronata var. *bismarckensis* Forel, 1901: 33. Holotype worker. Type locality: Bismarck Archipelago, Wunakokur (= Vunakokor [Mt Varzin], New Britain) (F. Dahl), MNHU (examined).

REMARKS. Comparison of the *P. mucronata* and *P. mucronata bismarckensis* holotypes clearly shows them to be representatives of distinct, separate species. The pronotal dorsum is relatively wide, with less prominent humeral teeth and distinctly more divergent propodeal spines in *P. bismarckensis*. However, the most obvious character separating these taxa involves the structure of their petioles. In *P. mucronata* the dorsolateral petiolar spines are rather slender and evenly curved, embracing the base of the first gastral segment. They have between them a pair of very short, posteriorly directed intercalary teeth. In *P. bismarckensis* the dorsolateral spines are relatively thick (thought not as massive as in *P. lucidula* Emery or *P. ridleyi* Forel — see below) and slightly curved at their bases; posteriorly the spines are almost straight, though slightly divergent, with their extreme apices distinctly bent outwards. The acute, obliquely rised intercalary teeth of *P. bismarckensis* are distinctly longer than those of *P. mucronata*.

Polyrhachis hortensis Forel, 1913 stat. nov.

Polyrhachis hippomanes var. *hortensis* Forel, 1913: 138. Syntype workers, queen, males. Type locality: Indonesia, Java, Buitenzorg (= Bogor) (H.v. Buttel-Reepen), MHNG (examined).

REMARKS. Comparison of the *P. hippomanes* and *P. hippomanes hortensis* types shows them to differ widely in a number of characters, including a distinctly more slender body and relatively much longer propodeal and petiolar spines in *P. hippomanes*. The head and mesosoma are also more densely punctate and opaque than in *P. hippomanes hortensis*, where the dorsal sculpturing is distinctly more shallow, with some shine evident on the occiput, at the bases of the propodeal and petiolar spines and over the gastral dorsum. The propodeum in *P. hippomanes hortensis* is relatively narrow, but less so than in *P. hippomanes*. It is armed with rather short, straight, divergent spines. The petiole of *P. hippomanes hortensis* has the lateral spines distinctly shorter, and there are two very short intercalary teeth, which are lacking in *P. hippomanes*. I am confident on these bases that *P. hortensis* represents a distinct species separate from *P. hippomanes*.

Polyrhachis lucidula Emery, 1893 stat. nov.

Polyrhachis hippomanes lucidula Emery, 1893: 254 (footnote). Holotype worker. Type locality: Burma, Tenasserim, Malewoon (L. Fea), MCSN (examined).

REMARKS. I have directly compared the holotypes of *P. hippomanes* and *P. hippomanes lucidula* and consider them to represent separate species. They differ in general appearance and in a number of other characters, including a distinctly more slender body, with relatively thin and long spines in *P. hippomanes*. The head and mesosoma are also rather densely punctate and opaque. In *P. lucidula* the body is wider, superficially sculptured and shiny. *P. lucidula* is obviously closely related to *P. ridleyi* Forel, and like that species it has remarkably massive petiolar spines. However, these two taxa differ in general appearance, with *P. lucidula* being consistently larger and considerably more shiny than *P. ridleyi*.

Examination of modern specimens from Sumatra and Java, which are comparable to *P. lucidula*, demonstrates some variability, notably in size. Even the largest specimen fails to attain the size of the holotype (HL 1.47 versus 1.53). However, all these specimens share an apparently distinctive, shiny appearance and colour pattern, involving a black body, dark brown antennae and light reddish-brown legs. In spite of their smaller size, the Sumatran specimens are very similar to the *P. lucidula* holotype, and I consider them to represent a conspecific population.

Polyrhachis moesta Emery, 1887

Polyrhachis hippomanes var. *moesta* Emery, 1887: 237. Holotype worker. Type locality: Indonesia, Sumatra, Sungei-Bulu (O. Beccari). MCSN (examined).

Polyrhachis paromalus tobias Forel, 1911: 391. Holotype worker. Type locality: Indonesia, Sumatra (Moesch), MHNG (examined). Syn. nov.

Polyrhachis moesta Emery; Wang & Wu, 1991: 599. Raised to species.

REMARKS. Forel noted the similarity between *P. paromalus tobias* and *P. hippomanes moesta*, but he had evidently not compared relevant specimens. I have compared the holotypes of both taxa and confidently declare them to be conspecific and taxonomically inseparable, despite some trivial differences, such as fractionally smaller humeral teeth and slightly less elevated propodeal spines in the *P. paromalus tobias* holotype.

Polyrhachis armata species-group
Polyrhachis caecilae Forel, 1912

Polyrhachis caecilae Forel, 1912: 76. Holotype worker. Type locality: Indonesia, Sumatra, Indrapura (Tritschler), MHNG (examined).

Polyrhachis (*Myrmhopla*) *punctata* Karavaiev, 1927: 36. Holotype worker. Type locality: Indonesia, Java, Buitenzorg (Karavaiev #2893). Syn. nov.

REMARKS. The holotype of *P. punctata* is conspecific with that of *P. caecilae*. The only apparent difference between them is the somewhat more solidly built mesosoma, with more downward curved pronotal spines, in *P. punctata*. The dorsal edge of the petiole between its lateral spines is furnished with three subequal intercalary teeth, with the middle tooth situated distinctly more forward than the other two, forming in dorsal view a clearly defined inverted 'v'. The colour of the body and appendages of these holotypes is essentially identical except for the gaster, which is distinctly more reddish in *P. caecilae*. The specific epithet stands as *P. caecilae* in the published original description, and that is formally the correct name for this species. The tag on the holotype, however, reads '*caeciliae*', and *P. caecilae* has been listed incorrectly under that name by all subsequent authors, including Emery (1925: 194), Dorow (1995: 47) and Bolton (1995: 345).

P. caecilae is closely related to *P. gestroi* Emery (1900: 714) and *P. gestroi rufiventris* Forel (1911: 391). However, as Forel (1912: 77) noted in the original description, *P. caecilae* differs from both species in having 3 intercalary teeth on the petiole, while there are only 2 in *P. gestroi* Emery and *P. gestroi rufiventris* Forel.

***Polyrhachis romanovi* Santschi, 1928 stat. nov.**

Polyrhachis (*Myrmhopla*) *acantha dichroa* Karavaiev, 1927: 33. Holotype worker. Type locality: Indonesia, Java, Bantam (W. Karavaiev), IZAS (examined). Junior primary homonym of *P. dichroa* Forel, 1893.

Polyrhachis (*Myrmhopla*) *acantha* st. *romanovi* Santschi, 1928: 139. Replacement name.

Polyrhachis saevissima romanovi Santschi; Dorow, 1995.

REMARKS. I have examined and directly compared the unique holotypes of *P. romanovi* and *P. saevissima* Fr. Smith, 1860, together with the types of *P. acantha* Fr. Smith, 1860 and *P. acasta* Fr. Smith, 1860, both of which were synonymised with *P. saevissima* by Bolton (1974: 178). I conclude that *P. romanovi* is obviously related to *P. saevissima* and bears a close resemblance, which is most direct with specimens meeting the *P. acasta* diagnosis. This similarity is accentuated by the almost identical colour pattern of the relevant specimens. However, the two species differ in several details, including the outline of the mesosoma, which is relatively high and evenly

curved in *P. romanovi*, while in *P. saevissima* and its cohorts (see below) the profile from the summit towards the propodeal spines is more-or-less sinuate, or almost straight, with a shallow depression at the promesonotal suture. The pronotal spines of *P. romanovi* are somewhat longer and more slender than those of *P. saevissima*, while the propodeal spines are shorter and the posterior face of the petiole distinctly more convex, in fact almost 'inflated'. The colouration of *P. romanovi* is distinctive, with the gaster and appendages light reddish-brown, in contrast to *P. saevissima*, specimens of which are totally black, apart from those formerly assigned to *P. acasta* (see above and under *P. saevissima* below). Comparison of the above specimens with recently collected material shows that these characters, including the colour scheme, are constant in specimens throughout the whole range of their distribution. It thus appears that assignment of specific rank to *P. romanovi* is appropriate.

I have also studied the types of *P. saevissima*, *P. acantha* and *P. acasta* (excluding their infraspecific forms) together with modern material from Sulawesi. Comparison shows *P. saevissima* to be relatively somewhat more slender than the others, with a distinctly narrower mesosomal dorsum (notably across the bases of the pronotal spines). The propodeal spines are also relatively more slender, and stand somewhat isolated. In *P. acantha* and *P. acasta* the bases of the spines are more broad and more-or-less medially contiguous. In profile the propodeal spines in *P. acasta* are strongly raised and virtually straight, while they are distinctly less elevated in the other two taxa. Those of *P. saevissima* are almost straight, while those of *P. acantha* are gently and evenly bent downwards. The petiolar spines in *P. acasta* closely embrace the first gastral segment, while in *P. acantha* the semicircle they form is distinctly more narrow. It is even more so in *P. saevissima*. Uniformly reticulate sculpturation of the mesosomal dorsum in *P. acantha* and *P. acasta* is almost hidden by abundant appressed pubescence, but this is rather dilute in *P. saevissima*. The colour of the body in these taxa is black, with the legs very dark brown to black, except in *P. saevissima*, where the apical portions of the tibiae are a shade lighter, and in *P. acasta*, where the trochanters, femora and tibiae are reddish-brown. I consider these three taxa to be very similar and almost certainly closely related. They appear to form numerous interlocking populations throughout their shared distributional range. As a result of these studies, and despite some

reservations, I currently follow Bolton (1974: 178) in considering *P. saevissima*, *P. acantha* and *P. acasta* to be putatively conspecific. I believe that the taxonomy of these entities could be competently resolved only following detailed study of worker-associated queens and consideration of the various (currently unavailable) relevant types of infraspecific forms.

Bolton (1974: 179) also suggested that the putatively closely related *P. diaphanta* Fr. Smith, 1861 could be a junior synonym of *P. saevissima*. However, concurrent examination of the relevant types has shown *P. diaphanta* obviously to be a distinct species. Its most characteristic feature is the sculpturation of the mesosoma, which is rather densely and deeply rugose-punctate, while merely uniformly reticulate in *P. saevissima*. The pronotal spines in *P. diaphanta* are short and thick, hardly longer than wide, while in *P. saevissima* they are distinctly more slender, and almost twice as long as wide at their bases. In *P. diaphanta* the mesosoma in profile rises strongly to the centre of the pronotum, then descends gently in a virtually straight, uninterrupted line towards the abrupt, almost vertical declivity. In contrast the outline of the mesosoma in *P. saevissima* is more-or-less sinuate, with a shallow depression at the promesonotal suture, and a gently raised mesonotum. The propodeal spines in *P. diaphanta* are relatively long and widely divergent, almost horizontal in profile and gently curved downwards. Their broadly contiguous bases bluntly divides the propodeal dorsum from the declivity. The petiolar dorsum bears a pair of strong, horizontal, relatively long, semicircular spines and two short, acute, dorso-posteriorly directed intercalary teeth. The petiolar spines in *P. diaphanta* embrace the first gastral segment, while in *P. saevissima* the semicircle formed by the spines is much narrower. On the inner surface of each spine in both species there is a distinct furrow, which runs from the base, adjacent to the intercalary teeth, almost to the tip. The colour of the body in *P. diaphanta* is black, with the legs very dark brown to black, in contrast to *P. saevissima*, where the colour of the legs ranges from relatively light reddish-brown to dark brown or black, with the tibiae a shade lighter. The antennae in *P. saevissima* are uniformly very dark brown or black, while in *P. diaphanta* the funiculus is distinctly bicoloured. The first segment is black, save for a narrow, light, apical band. The width of such light coloured bands progressively increases through the series of more distal segments, with the five apical segments entirely light

yellowish-brown. *P. diaphanta* appears to be rather uncommon. I have seen only one other specimen closely comparable to its type.

***Polyrhachis sexspinosa* species-group**
***Polyrhachis esuriens* Emery, 1897 stat. nov.**

Polyrhachis sexspinosa var. *esuriens* Emery, 1897: 591. Syntype workers, queen. Type locality: New Guinea (L. Loria), MCSN, QMBA (examined).

Polyrhachis sexspinosa var. *esuriens* Emery; Bolton, 1975: 12. Junior synonym of *P. sexspinosa* (Latreille, 1802: 126).

Polyrhachis (Myrmhopla) arcuspinosa Donisthorpe, 1941: 140, fig. 1. Syntype workers. Type locality: New Guinea, Mt Nomo, S of Mt Bougainville (L.E. Cheesman), BMNH, QMBA (examined). Syn. nov.

Polyrhachis (Myrmhopla) juxtaspinosa Donisthorpe, 1949: 417, fig. 2. Syntype workers. Type locality: New Guinea, Maffin Bay (E.S. Ross), CAS, BMNH (examined). Syn. nov.

REMARKS. Bolton (1975: 12) considered *P. sexspinosa esuriens*, *P. arcuspinosa* and *P. juxtaspinosa* (and several other names), to be synonymous under *P. sexspinosa* (Latreille). I have examined the syntypes of these three taxa, in comparison with the voucher specimen ('paradigm') of *P. sexspinosa* in QMBA (Kohout & Taylor, 1990: 519-520) and I am confident that, while they are clearly conspecific, they are not synonymous with *P. sexspinosa*. The syntypes of these taxa differ from the *P. sexspinosa* paradigm in a number of characters, including distinctly more gracile stature and more slender spines. The petiole has a flat, anteriorly sloping dorsum and more-or-less horizontal, barely elevated, posteriorly directed spines, situated at the apex of the posterior face of the segment. The propodeal spines are very variable in length and degree of elevation, though mostly strongly inclined posteriorly and either parallel or diverging with their tips curved downwards. In *P. sexspinosa* the body is generally more robust and the petiole has a distinctly convex dorsum, with spines rising obliquely from their bases, which are situated well below the apex of the dorsal convexity. The propodeal spines appear less variable, and are mostly vertical or inclined forwards or backwards, and generally straight with only their tips slightly curved. The mainly golden pubescence of *P. esuriens* (including *P. arcuspinosa* and *P. juxtaspinosa*) almost hides the underlying sculpturation, except on the propodeal dorsum, where it is usually somewhat diluted, exposing the characteristic reddish colour of the body. In contrast, the pubescence in *P. sexspinosa* is off-white to silvery, and the body mostly black.

***Polyrhachis waigeuensis* Donisthorpe, 1943
stat. nov.**

Polyrhachis (*Myrmhopla*) *arcuspinosa waigeuensis* Donisthorpe, 1943: 467. Syntype workers. Type locality: New Guinea, Waigau I., Cape Nok (L.E. Cheesman), BMNH (examined).

Polyrhachis (*Myrmhopla*) *arcuspinosa waigeuensis* Donisthorpe; Bolton, 1975: 12. Junior synonym of *P. sexspinosa* (Latrille, 1802: 126).

REMARKS. Comparison of the syntypes of *P. arcuspinosa waigeuensis* with types and other specimens of closely related taxa of the *P. sexspinosa*-complex indicated that they represent a 'good' species. *P. waigeuensis* stands between *P. esuriens* and *P. sexspinosa*, sharing with *P. esuriens* a flat-topped petiole with barely elevated, posteriorly directed spines, and with *P. sexspinosa* a relatively robust body. However, *P. waigeuensis* differs from both these species (and others of the complex) by a highly convex pronotal dorsum. Subsequent examination of abundant recent material, including several nest series (PNG, West Sepik Prov., Pes Mission, c. 12km WSW of Aitape, 03°11'S, 142°15'E, 31 vii-3 viii 1984; Torricelli Mts, Lumi, 03°28'S, 142°02'E, 4-13 viii 1984; Madang Prov., Naru, Gogol Riv., 20km SW of Madang, 05°21'S, 145°41'E, 22 viii 1984 [all R.J. Kohout]), shows the pronotum ranging from moderately to highly convex, even almost dome-shaped in some individuals. However, despite this variability, it seems always to be higher than in other species of the complex, and this provides a dependable character, setting *waigeuensis* well apart. I thus recommend its separate specific status.

Subgenus *Myrma* Billberg, 1820

***Polyrhachis continua* species-group**

***Polyrhachis conops* Forel, 1901**

Polyrhachis conops Forel, 1901: 28. Syntype workers, queens, males. Type locality: Bismarck Archipelago, Herbertshöhe (F. Dahl), MNHU, MHNG, QMBA (examined).

Polyrhachis (*Myrma*) *conops* var. *bismarckensis* Karavaiev, 1927: 46. Holotype worker. Type locality: Bismarck Archipelago, ?MNHU, ?IZAS (location of type unknown). Junior primary homonym of *P. mucronata bismarckensis* Forel, 1901: 33.

Polyrhachis (*Myrma*) *conops* var. *stitzi* Santschi, 1928: 139. Replacement name. Syn. nov.

REMARKS. The holotype of *P. conops stitzi* cannot be found in the Karavaiev collection (IZAS), or in the Stitz collection (MNHU). It appears to have been lost. However, during a recent visit to MNHU I located a small bottle containing six unidentified specimens referable to the *P. continua* species-group, labelled 'Ralum Dahl'. The series comprised two workers and four late queens,

all callows at various stages of pigmentation. However, the workers and two of the queens were suitable for dry mounting. Their later comparison with Karavaiev's brief description, strongly indicates that they are in fact identifiable as *P. conops stitzi*. Judging from the original description ('Gastersegmente, vom dritten an, dunkel ockerfarben'), the *P. conops stitzi* holotype was also callow. It seems reasonable to conclude that the aforementioned specimens are the remainder of the series from which Stitz supplied one specimen to Karavaiev (1927: 46). Their comparison with the syntypes of *P. conops* shows these forms to be essentially identical and undoubtedly conspecific.

***Polyrhachis continua* Emery, 1887**

Polyrhachis continua Emery, 1887: 235, pl. 4, fig. 21.

Holotype worker. Type locality: Indonesia, Ternate, Aquí Conora (O. Beccari), MCSN (examined). [Specimens from Paumotu River (= Angabanga Riv.), New Guinea, L. Loria (Emery det. & coll., MCSN) are wrongly labelled as types].

Polyrhachis continua var. *revocata* Viehmeyer, 1913: 151. Syntype workers. Type locality: Indonesia, Sulawesi (in copal), MNHU (examined). Syn. nov.

REMARKS. Comparison of the *P. continua* holotype with *P. continua revocata* syntypes shows them to be very similar. In both the clypeus is almost straight, with only a shallow depression at the distinctly medially truncate anterior margin. The frontal carinae are markedly close together, leaving the central area rather narrow, and scarcely widened towards the occiput. However, in *P. continua*, the somewhat flattened pronotal spines are shorter, relatively less divergent and minutely emarginated at their bases, while *P. continua revocata* has longer, distinctly more divergent spines, which have their dorsolateral borders continuous posteriorly in uninterrupted alignment with the pronotal margins. The petiolar spines are also slightly longer than in *P. continua*. The head and mesosoma in *P. continua* are very finely, more-or-less regularly, striate-punctate. The sculpturation in *P. continua revocata* is somewhat more distinct and more regular. However, when the types are compared to other New Guinean specimens referable to *P. continua*, it is clear that the characters putatively separating these forms fall well within the limits of variation represented in the material. I therefore conclude that the names *P. continua* and *P. continua revocata* together refer to a single biological species.

***Polyrhachis procera* Emery, 1897 stat. nov.**

Polyrhachis continua var. *procera* Emery, 1897: 581. Syntype workers, queens. Type locality: New Guinea, Havcri (L. Loria), MCSN (examined).

REMARKS. Emery (1897) separated *P. procera* from *P. continua* on the basis of its larger size and the more pronounced striation of its head and thorax ('... sono più grandi e con striatura del capo e del torace più marcata'). However, direct comparison of the types evidences differences in a number of other characters. In *P. procera* the clypeus in profile is gently sinuate, with the anterior margin vaguely obtuse medially (entire in modern specimens) and the medial carina distinct for most of its length. In contrast the clypeal border in *P. continua* is almost straight, with only a shallow depression at the anterior margin, which is distinctly medially truncate. The pronotal spines in *P. procera* are relatively long and more slender, with the lateral margins of mesonotal dorsum clearly converging anteriorly, and its posterior angles broadly rounded. The leading edges of the antennal scapes of *P. procera* carry a few hairs, which are totally lacking in *P. continua*. Comparable pilosity in both species is limited to the head and gaster, where it is rather diluted dorsally. *P. procera* is black with dark reddish-brown appendages, with the tibiae and apical segments of the funiculi a shade lighter. In *P. continua* the colour scheme is similar, except that the appendages are generally light reddish-brown. Examination of the types and other available material clearly demonstrates that *P. procera* is a 'good' species distinct from *P. continua*.

***Polyrhachis sericeopubescens* Donisthorpe, 1941**

Polyrhachis (Myrma) sericeopubescens Donisthorpe, 1941: 61. Syntype worker, queen. Type locality: New Guinea, Japen I., Mt Baduri (for ♀); Mt Eiori (for ♀) (L.E. Cheesman), BMNH (examined).

Polyrhachis inusitata Kohout, 1989: 513, figs 4, 5, 9. Holotype, paratype workers. Type locality: Australia, Qld, Cape York Peninsula, Iron Range (G.B. Monteith & D. Cook), QMBA, ANIC. Syn. nov.

REMARKS. I have examined a syntype worker of *P. sericeopubescens* and the holotype and two paratypes of *P. inusitata*. Despite some relatively minor differences they are remarkably similar. Both taxa appear to be very rare. The only known specimens are their respective type series. The type localities are separated by a great distance, and no specimens have been recorded from intervening areas. However, because of their similarity, I believe these two nominal taxa to represent separate populations of a single biological species.

***Polyrhachis simpla* Santschi, 1928 stat. nov.**

Polyrhachis (Myrma) conops simplex Karavaiev, 1927: 45. Syntype workers, queens, males. Type locality: Indonesia, Aru Is, Wammar I. (W. Kara-

vaiev), IZAS, QMBA (examined). Junior primary homonym of *P. simplex* Mayr, 1862: 682.

Polyrhachis (Myrma) conops st. simpla Santschi, 1928: 139. Replacement name.

REMARKS. I have examined syntypes of *P. simpla* together with syntypes of *P. continua* Emery, *P. continua hirsutula* Emery, *P. conops* Forel and *P. conops spinifera* Stitz, and believe *P. simpla* to represent a species separate from the others. Its type stands closest to those of *P. conops spinifera*, sharing with them a relatively wide pronotal dorsum. However, the lateral pronotal margins in *P. conops spinifera* are distinctly raised, while those of *P. conops simpla* are rather flat. The lateral margins of the mesonotal and propodeal dorsa in *P. conops simpla* are more strongly converging posteriorly, with the pilosity much diluted, producing a rather graceful appearance, in comparison with the more robust and rather hairy *P. conops spinifera*. Further examination of abundant modern material confirms these characters to be constant, justifying the elevation of *P. conops simpla* to specific rank.

***Polyrhachis spinifera* Stitz, 1911 stat. nov.**

Polyrhachis conops var. *spinifera* Stitz, 1911: 376, fig. 22b. Syntype workers. Type locality: New Guinea, Tana (Moszkowski), MNHU, MHNG (examined). *Polyrhachis continua* var. *hirsutula* Emery, 1911: 256. Syntype workers. Type locality: New Guinea, R. Digul (= ?Digoel Riv.), MCSN (examined). Syn. nov.

REMARKS. Direct comparison of *P. conops spinifera* and *P. continua hirsutula* syntypes shows them to be very similar, undoubtedly representing a single species. They differ from *P. conops* and *P. continua* by possessing a markedly wider pronotal dorsum and rather abundant semierect to erect pilosity, which is almost completely lacking in these other species.

Stitz (1911: 376, fig. 22c) also described a very similar taxon, *P. conops cuspidata*, in the same article as *P. conops spinifera*. He specified the shape of the petiole, with shorter and divergent petiolar spines and a rather narrow 'thorax' as the main characters separating *P. cuspidata* from *P. spinifera*. Comparison of the syntypes of these nominal taxa to investigate their relative status has proved somewhat inconclusive. Examination of numerous specimens of various *P. continua*-group species, including several nest series of the closely allied *P. simpla* Santschi (see above), has shown a degree of variability in all of the characters given for *P. cuspidata* and *P. spinifera* by Stitz, but never sufficient to bridge the difference

in width of the pronotal dorsum separating their types. I therefore hesitate to consider them conspecific. Only study based on material additional to that now available could establish the true status of *P. conops cuspidata*.

***Polyrhachis relucens* species-group
Polyrhachis andromache Roger, 1863**

Polyrhachis hector Fr. Smith, 1859: 142. Holotype worker. Type locality: Indonesia, Aru Is (A.R. Wallace), OXUM (examined). (Junior primary homonym of *P. hector* Fr. Smith, 1857: 62).

Polyrhachis andromache Roger, 1863b: 8. Replacement name.

Polyrhachis (Myrma) proxima var. *semirufipes* Donisthorpe, 1943: 469. Holotype worker. Type locality: New Guinea, Waigeu, Camp Nok (L.E. Cheesman), BMNH (examined). Syn. nov.

**Polyrhachis (Myrma) sericata pruinosa* var. *harmsi* Karavaiev, 1930: 212. Workers. Original locality: New Guinea (F. Weyer), IZAS (examined). Unavailable name.

(For full reference citations see Kohout, 1988: 430.)

REMARKS. Direct comparison of the *P. proxima semirufipes* and *P. andromache* holotypes, together with a single worker of the '*P. sericata pruinosa harmsi*' original series, shows them undoubtedly to be conspecific. Within the whole range of distribution (which extends from the eastern Indonesian islands, throughout New Guinea, and southwards to Cape York Peninsula in northern Australia) the general appearance of *P. andromache* seems rather constant. Variability appears to be confined to the color of the rather smooth, appressed pubescence, which ranges from silvery to a rich golden colour.

***Polyrhachis decipiens* Roger, 1863 stat. nov.**

Polyrhachis decipiens Roger, 1863a: 156. Syntype workers. Type locality: Indonesia, Batjan I., MNHU (examined).

Polyrhachis relucens decipiens Roger; Emery, 1897: 580.

Polyrhachis restituta Viehmeyer, 1913: 149. figs. Syntype workers. Type locality: Indonesia, Sulawesi (in copal), MNHU (examined). Syn. nov.

Polyrhachis restituta var. *conclusa* Viehmeyer, 1913: 151, fig. Holotype worker. Type locality: Indonesia, Sulawesi (in copal). MNHU (examined). Syn. nov.

REMARKS. Direct comparison of all the relevant, essentially identical, types shows the above nominal taxa undoubtedly to be conspecific. The characters given by Viehmeyer to separate *P. restituta* and *P. restituta conclusa* are trivial, and these names undoubtedly cover a single, albeit variable, biological species. There are slight differences in the length and direction of the pronotal

spines. According to the original illustration, the dorsolateral petiolar spines in *P. restituta conclusa* are distinctly shorter than in the other taxa. In reality, however, the spine conforming to the figure has the tip broken off - the other is only a fraction shorter than those of the *P. restituta* type. Marginal differences are evident in the width of the propodeal dorsum, which, in *P. restituta conclusa*, is relatively a little narrower, with the lateral margins more-or-less parallel, where in *P. restituta* they converge slightly posteriorly. These characters, however, are known to be intergradient throughout species of the subgenus *P. (Myrma)*, and seem only to emphasise the variability among its species.

***Polyrhachis foreli* Kohout, 1989**

Polyrhachis foreli Kohout, 1989: 510, figs 2, 2a, 11. Holotype worker, paratype workers, queens, males. Type locality: Australia, Qld, NE Tully, nr Clump Pt (R.W. Taylor, acc. 69.123), ANIC, QMBA (for a full list of depositories see Kohout, 1989: 510) (examined).

**Polyrhachis (Myrma) relucens* r. *andromache* var. *andromeda* Forel, 1915: 110. Workers. Original locality: Australia, Qld, Bellenden Ker (E. Mjöberg), NRMS, MHNG, ANIC (examined). Unavailable name.

**Polyrhachis relucens deciptens* var. *papuana* Emery, 1897: 580. Workers, queens. Original localities: New Guinea, Dilo, Bara Bara, Goodenough I. (L. Loria), MCSN, MHNG (examined). Unavailable name.

REMARKS. In a review of the Australian ants of the *Polyrhachis relucens* species-group (Kohout, 1989: 512) I noted that the specimens described by Emery (1897: 580) as '*P. relucens deciptens papuana*' are remarkably similar to those of Forel's infrasubspecies '*P. relucens andromache andromeda*' which I considered conspecific with *P. foreli*. I did not absorb Emery's form within *P. foreli* because of features exhibited by the available single queen (Kohout, 1989: 512-513). These quadrinomens cannot, of course, be formally recognised in animal nomenclature, and are technically unavailable. However, I have since located in the Emery and Forel collections 11 specimens of the original '*Polyrhachis relucens deciptens papuana*' series, consisting of 7 workers and 4 queens. Comparison of these specimens, including 3 queens, with *P. foreli* material shows them definitely to be conspecific. However, the single queen examined earlier (see above & Kohout, 1989) clearly represents a different species. I am therefore confident in suggesting that the unavailable name '*P. relucens deciptens papuana*'

was originally applied to New Guinean material of *P. foreli*.

***Polyrhachis litigiosa* Emery, 1897 stat. nov.**

Polyrhachis relucens litigiosa Emery, 1897: 581. Syntype workers. Type locality: New Guinea, Paimomu Riv. (= Angabanga Riv.) (L. Loria), MCSN (examined).

Polyrhachis (Myrma) sericata pruinosa Karavaiev, 1927: 48. Syntype workers. Type locality: Indonesia, Aru Is, Wammar I. (W. Karavaiev #2618), IZAS, QMBA (examined). Junior primary homonym of *P. pruinosa* Mayr, 1872.

Polyrhachis (Myrma) sericata var. *pruinosa* Santshii, 1928: 139. Replacement name. Syn. nov.

REMARKS. I have compared the syntypes of *P. relucens litigiosa* with a voucher specimen previously compared to the holotype of *P. relucens* and am confident that they represent separate biological species. *P. relucens litigiosa* is consistently distinguished by its more gracile stature and transversely narrow petiole, with slender, somewhat diverging dorsolateral spines. In contrast the body of *P. relucens* is distinctly broader, notably across the pronotal dorsum and petiole. The latter is armed with a pair of relatively thick spines and a distinct intercalary tooth. Mostly golden, appressed pubescence covers all body surfaces in both species; erect golden hairs are abundant in *P. litigiosa*, but sparse in *P. relucens*, where they are confined to the head, lateral portions of mesosoma and the gaster. Subsequent comparison of *P. sericata pruinosa* and *P. litigiosa* specimens shows them to be virtually identical and straightforward synonyms.

***Polyrhachis nigropilosa* Mayr, 1872**

Polyrhachis nigropilosa Mayr, 1872: 141. Syntype workers. Original localities: Indonesia, Sulawesi (Stevens); Borneo, Sarawak (J. Doria), NHMW (examined).

Polyrhachis nigropilosa var. *conophthalma* Emery, 1900: 713. Holotype worker. Type locality: Indonesia, Sumatra (E. Modigliani), MCSN (examined). Syn. nov.

REMARKS. I have compared the syntypes of *P. nigropilosa* with the holotype of *P. nigropilosa conophthalma* and abundant modern material. Apart from the shapes of their eyes no possibly significant differences between the two taxa could be found. They are remarkably similar and, moreover, a short series of specimens collected at Gombak Forest Reserve, Malaysia (USNM), demonstrates a gradual transition from strongly to rather weakly conical eyes. As mentioned below under *P. rixosa* Fr. Smith, the peculiar ten-

dency of the eyes to vary from 'normal' to posteriorly elongated, or posteriorly truncated, is prominent in several species of subgenus *P. (Myrma)*, and I conclude that these names have been applied to a single biological species.

***Polyrhachis noesaensis* Forel, 1915 stat. nov.**

Polyrhachis villipes var. *noesaensis* Forel, 1915a: 43 (footnote). Syntype workers. Type locality: Indonesia, Java, Nusa Kambangan (E. Jacobson), MHNG (examined).

REMARKS. Direct comparison of the *P. villipes* holotype and a syntype of *P. villipes noesaensis* reveals that they represent distinct species. The former is generally smaller, with the mesosomal dorsum finely longitudinally striate and the petiole with relatively short dorsolateral spines and an almost straight dorsal edge. Rather diluted, silvery, appressed pubescence covers most of the body, except on dorsum of the first gastral segment, where the pubescence has a distinctly reddish tint. In *P. noesaensis* the mesosomal dorsum is very finely shagreened and rather shiny, with only scattered piliferous pits, from which the relatively short, bristle-like pilosity arises. The dorsal edge of the petiole is concave between rather long, moderately diverging spines. The mostly golden or silvery, appressed pubescence is rather dilute on the dorsal surface of the mesosoma and completely absent from the gaster which, besides the piliferous pits, is smooth and shiny. Due to these obvious dissimilarities I am confident in considering *P. noesaensis* a species distinct from *P. villipes*.

***Polyrhachis obesior* Viehmeyer, 1916 stat. nov.**

Polyrhachis mayri var. *obesior* Viehmeyer, 1916: 165. Syntype workers. Original localities: West Malaysia, Melaka, Gunong Angsi; Singapore (H. Overbeck), MNHU (examined).

Polyrhachis illaudata obesior Viehmeyer; Dorow, 1995: 35.

REMARKS. I have compared the holotype of *P. illaudata* Walker (BMNH) with syntypes of *P. mayri obesior* and specimens of *P. mayri* Roger (both MNHU) and am confident that, while *P. illaudata* and *P. mayri* are clearly conspecific (Bolton, 1974: 176), *P. mayri obesior* represents a separate species. In spite of its similar appearance, *P. obesior* is generally relatively robust, with a broadly transverse petiole, which has a distinct intercalary tooth in the centre of its dorsal edge. In lateral view the bases of the dorsolateral spines are situated close to the posterior face of

the petiole, with the spines rising obliquely, and their tips turned slightly downwards. Consequently, the dorsal edge of the petiole, in lateral view, is clearly visible and very prominent. In contrast the petiole in *P. illaudata* is narrowly transverse and, in lateral view, the dorsal petiolar edge is virtually hidden by the more-or-less upright dorsolateral spines. Examination of numerous, mostly recently collected, specimens shows the characters separating these species to be constant and I confidently raise *P. obesior* to specific rank.

***Polyrhachis obliqua* Stitz, 1911 stat. nov.**

Polyrhachis labella var. *obliqua* Stitz, 1911: 375, fig. 21. Syntype workers. Type locality: Solomon Is., Bougainville I. (= PNG, Nth Solomons Prov.) (H. Schoede S.G.), MNHU (examined).

'*Polyrhachis relucens* r. *litigiosa* var. *aloseana*' Forel, 1901: 28. Workers, queen. Original locality: Bismarck Archipelago, Wunakokur nr Ralum (F. Dahl), MNHU, MHNG, QMBA (examined). Unavailable name.

REMARKS. Comparison of the *P. labella* holotype and syntypes of *P. labella obliqua* shows them to be very dissimilar, clearly representing separate species. In *P. labella*, the sides of the head behind the eyes are gently convergent posteriorly, while in *P. obliqua* they are broadly convex. The leading edges of the antennal scapes in *P. obliqua* bear numerous short erect hairs, which are completely absent in *P. labella*. Moreover, in *P. obliqua* the pronotal spines are divergent from their bases, and the dorsum of the petiole is armed with slender, slightly diverging dorsolateral spines and a more-or-less distinct, small intercalary tooth. In *P. labella* the pronotal spines are directed forwards, the petiole is armed with a pair of relatively long, fairly thick, subparallel spines, and the dorsal edge of the segment is concave, with no indication of intercalary teeth.

Comparison of the *P. obliqua* syntypes and the original series of '*P. relucens litigiosa aloseana*', together with abundant modern material (including several nest series) from Guadalcanal and Bougainville I. to New Britain and New Ireland, clearly shows these forms to be conspecific.

***Polyrhachis rixosa* Fr. Smith, 1858**

Polyrhachis rixosus Fr. Smith, 1858: 68. Holotype queen. Type locality: Indonesia, Sulawesi, BMNH (examined).

Polyrhachis lycidas Fr. Smith, 1861: 43, pl. 1, fig. 23. Holotype worker. Type locality: Indonesia, Sulawesi, Tondano (A.R. Wallace), OXUM (examined). Syn. nov.

REMARKS. Comparison of both relevant types and a series of modern specimens from Dumoga-Bone, Sulawesi, comprising workers and an alate queen, confirms their synonymy and demonstrates that *P. lycidas* is the worker of *P. rixosa*. The recently collected queen compares well with the *P. rixosa* holotype — the only noticeable differences being the somewhat shorter pronotal spines of the holotype and slightly different configuration of the petiolar spines. In the holotype the dorsolateral spines and the intercalary tooth are equal in size, while in the Dumoga-Bone specimen the dorsolateral spines are distinctly longer, with the intercalary tooth much reduced. The Dumoga-Bone workers compare well with the holotype of *P. lycidas* — the only apparent variability being in the thickness of the pronotal spines, intensity of longitudinal striation on the mesosomal dorsum and configuration of the petiolar spines, the intercalary tooth being less distinct in some specimens than others. In the holotype and several specimens of the Dumoga-Bone series the eyes show a mild tendency towards posterior protraction, a feature not uncommon in species of subgenus *P. (Myrma)* (see above under *P. nigropilosa* Mayr).

P. rixosa is very similar to *P. sculpturata*. However, the dorsolateral petiolar spines in *P. rixosa* are much shorter, and the dorsal edge of the petiole bears a more-or-less distinct intercalary tooth which is completely lacking in *P. sculpturata*. Also, in *P. sculpturata* the pronotal spines are distinctly longer and more slender and divergent than in *P. rixosa*.

***Polyrhachis rufofemorata* Fr. Smith, 1859**

Polyrhachis rufofemoratus Fr. Smith, 1859: 142. Holotype worker. Type locality: Indonesia, Aru Is (A.R. Wallace), OXUM (examined).

Polyrhachis merops Fr. Smith, 1860b: 98, pl. 1, fig. 17. Holotype worker. Type locality: Indonesia, Batjan I. (A.R. Wallace), OXUM (examined). Synonymy by Bolton (1974: 178).

Polyrhachis biroï Forel, 1907: 40. Holotype worker. Type locality: Indonesia, Ambon I. (L. Biró), HNHM (examined). Syn. nov.

Polyrhachis biroï var. *bidentata* Stitz, 1912: 512. Syntype workers. Type locality: New Guinea (Lauterbach), HNHM, MHNG (examined). Syn. nov.

Polyrhachis biroï var. *paprika* Forel, 1911: 296. Holotype worker. Type locality: Indonesia, Waigiou I. (Bates), ZSSM (examined). Syn. nov.

REMARKS. Comparison of the types listed above demonstrates that all fall within the parameters of *P. rufofemorata* variability, as discussed by Kohout (1989: 514). The specimens differ primarily in the development of the petiolar node which, in *P. rufofemorata*, *P. merops*, *P.*

biroi and *P. biroi paprika*, is simply angulate or at most minutely dentate, while it is clearly bispinose in *P. biroi bidentata*. Some series exhibit occasional variability in the length and thickness of the pronotal spines, with Indonesian specimens (Seram, Ambon I.) having relatively long, more slender pronotal spines than their New Guinean and Australian counterparts. However, when specimens from the whole range of distribution are considered, no taxonomically significant variability can be detected — the above synonymy follows readily.

***Polyrhachis sculpturata* Fr. Smith, 1860**

Polyrhachis sculpturatus Fr. Smith, 1860a: 70. Syntype worker, queen. Type locality: Indonesia, Sulawesi, Makassar (A.R. Wallace). OXUM (worker examined).
Polyrhachis sumatrensis r. *hamulata* Emery, 1887: 234. Syntype workers, queen. Type locality: Indonesia, Sulawesi, Kandari. iii 1874 (O. Beccari). MCSN (worker examined). Syn. nov.

REMARKS. Emery was evidently unaware of *P. sculpturata* when he described *P. sumatrensis hamulata*. Comparison of the types shows these forms to be essentially identical and undoubtedly conspecific.

***Polyrhachis semitestacea* Emery, 1900
stat. nov.**

Polyrhachis andromache var. *semitestacea* Emery, 1900: 334. Syntype workers. Type locality: New Guinea, Friedrich-Wilhelmshafen (= Madang) (L. Biró), HNHM, MCSN, QMBA (examined).

REMARKS. I have compared the holotype of *P. hector* Fr. Smith, 1859 (= *P. andromache* Roger, 1863) with syntypes of *P. andromache semitestacea* Emery, and abundant modern material comprising several complete nest series, and am confident that these types represent separate, distinct species. The differences separating them are rather subtle, but appear to be constant and to set both species apart. *P. semitestacea* is characterised by more gracile stature, petiole with dorsal spines closer together and without an intercalary tooth, and by the distinctly light honey-yellow colour of the gaster, which is covered with very pale appressed pubescence. *P. andromache* appears generally more robust with the colour and pubescence of the gaster matching that of the rest of the body. The petiolar spines are further apart than in the *P. semitestacea* types, and the dorsal edge of the petiole is furnished with a minute intercalary tooth.

***Polyrhachis striata* Mayr, 1862**

Polyrhachis striatus Mayr, 1862: 686, pl. 19, fig. 8 (1865: 44, pl. 2, figs 11a, b, c). Syntype workers.

Type locality: Indonesia, Java (Novara Exp.; Kirsch & Thorey), NHMW (examined).

Polyrhachis striata r. *assamensis* Forel, 1902a: 289. Syntype workers. Type locality: India, Assam (Smythies), MHNG (examined). Syn. nov.

REMARKS. Forel separated the race *P. striata assamensis* from *P. striata* principally on the basis of its more robust build, less divergent pronotal spines, more dense and more regular striations and the lack of lateral longitudinal ridges on the gaster ('Abdomen ... sans trace de rides longitudinales.'). However, following comparison of the available types of both names I find Forel's statement to be not entirely accurate. Although relatively less prominent than in *P. striata*, the lateral gastral ridges are more-or-less evident in all *P. assamensis* syntypes examined. Forel's reference to the less divergent pronotal spines in *P. striata assamensis* holds for the types, but abundant recent material indicates gradual transition between the extremes. Examination of the types together with modern material shows that this variation clearly falls well within the limits expected in a species with such a wide distributional range. I have no hesitation in considering *P. striata* and *P. striata assamensis* conspecific.

***Polyrhachis striatorugosa* Mayr, 1862
stat. rev.**

Polyrhachis striatorugosus Mayr, 1862: 686, pl. 19, fig. 9. Syntype workers. Type locality: Indonesia, Java (Sichel), NHMW (examined).

Polyrhachis sumatrensis r. *striatorugosa* Mayr; Emery, 1887: 234 (footnote). Reduced in rank to race of *P. sumatrensis* Fr. Smith.

Polyrhachis sumatrensis striatorugosa Mayr; Emery, 1925: 203.

Polyrhachis striatorugosa var. *exophthalma* Forel, 1913: 136. Syntype worker, queens. Type locality: Indonesia, Sumatra, Beras Tagi. Bandar Baroe (H.V. Buttel-Reepen), MHNG (examined). Syn. nov.

REMARKS. I have examined the holotype queen of *P. sumatrensis*, a syntype worker of *P. striatorugosa*, and specimens from Java (including a queen), and consider that Emery's reduction of *P. striatorugosa* to a subspecies of *P. sumatrensis* was unjustified. As mentioned elsewhere in this paper, I deem *P. sumatrensis* to be conspecific with *P. villipes* Fr. Smith. Consequently, I have no hesitation in reinstating *P. striatorugosa* to its original specific rank.

Further comparison of the *P. striatorugosa* syntype with syntypes of *P. striatorugosa exophthalma* and available specimens from Java and Sumatra shows clearly that all represent a single species. As its name suggests, the eyes of *P.*

striatorugosa exophthalma are neither prominent nor posteriorly protracted. In all other aspects, however, it and *P. striatorugosa* are closely similar. I regard them as conspecific.

***Polyrhachis vestita* Fr. Smith, 1860**

Polyrhachis vestitus Fr. Smith, 1860a: 71. Holotype worker. Type locality: Indonesia, Sulawesi, Makassar (A.R. Wallace), OXUM (examined).

Polyrhachis vestita var. *unicolor* Emery, 1898: 242. Syntype workers. Type locality: Indonesia, Sulawesi, (H. Fruhstorfer), MCSN (2 examined). Syn. nov.

REMARKS. I have compared the types of *P. vestita* and *P. vestita unicolor* together with numerous recently collected specimens. Despite their similar general appearance they vary in many details. The eyes of both types are moderately convex, and only marginally exceed the lateral cephalic outline in frontal view, while those of modern specimens from Dumoga-Bone Nat. Park, Sulawesi, range from moderately convex (in dark-legged specimens) to strongly convex (in light-legged specimens), extending clearly beyond the outline of the head. In a series of specimens from Lore-Lindu Nat. Park, Sulawesi, however, the eyes are only weakly convex and do not attain the cephalic borders in full-face view. The antennae are relatively longer (SI 192-200) in the type of *P. vestita* (and dark-legged specimens from Dumoga-Bone), than in the type of *P. vestita unicolor* (and light-legged specimens from Dumoga-Bone and Lore-Lindu material) (with SI 172-185). In profile the anterior portion of the clypeus ranges from almost straight to shallowly or distinctly concave, with the basal margin only shallowly impressed, and the anterior margin entire and only occasionally shallowly truncated medially. The lateral margins of the pronotal dorsum are almost parallel, but, in some specimens, they converge anteriorly and are widely but shallowly emarginate at the bases of the horizontal, anteriorly or anterolaterally projecting pronotal spines. The mesonotum is more-or-less transverse, with the lateral margins parallel or slightly convergent posteriorly. The propodeal dorsum is almost quadrate, sloping posteriorly in a gentle curve towards the declivity. The posterior propodeal angles are produced as short upturned denticles, which are rather obscure in some specimens from Dumoga-Bone, but distinct and well defined in specimens from Lore-Lindu. However, intermediates are common, and in both types the posterior angles are only moderately distinct. The transition between the propodeal dorsum and declivity is either medially

uninterrupted, or in some specimens there is a rather indistinct 'U' shaped transverse carina vaguely dividing the faces. The petiole is scale-like, with the lateral angles ranging from indistinct to short, upturned, rather acute teeth. The dorsal edge of the petiole is mostly semicircular and entire, though in many specimens it is somewhat obtusely angulate, with a single or double shallow emargination in the centre. In specimens from Lore-Lindu, an additional pair of dorsolateral teeth is situated just above the lateral angles, and the dorsal edge is almost straight or weakly bowed and medially emarginate. The types and most specimens examined are totally black, but in a short series from Dumoga-Bone the trochanters and femora, save for their extreme distal ends, are light reddish-yellow. The appressed pubescence ranges from silvery, with a greenish or yellowish tint, to a rich golden hue. The mostly golden, medium to long pilosity varies from rather dilute to dense, covering most of the body, except in the specimens from Lore-Lindu, where it is almost completely absent from the dorsa of the gaster and petiole.

It is obvious that Emery, when describing *P. vestita unicolor*, considered the bicoloured form of this species to be typical *P. vestita*. However, the types of both taxa are in fact unicoloured with black legs and, considering the variability of this species, I am confident that *P. vestita unicolor* is taxonomically inseparable from *P. vestita*, and that both should be treated as a single, albeit rather variable, species.

***Polyrhachis vigilans* Fr. Smith, 1858**

Polyrhachis vigilans Fr. Smith, 1858: 69, pl. 4, fig. 39. Holotype queen. Type locality: China, Hong Kong, BMNH (examined).

Polyrhachis (Myrma) vigilans Fr. Smith; Donisthorpe, 1937: 626, fig. 7. Description of worker.

Polyrhachis pyrgops Viehmeyer, 1912: 9, fig. 10. Holotype worker. Type locality: China, DEIE (examined). Syn. nov.

REMARKS. Bolton (1995: 355) erroneously listed the provenance of *P. pyrgops* as New Guinea, probably because the original description was published in a paper entitled 'Ameisen aus Deutsch Neuguinea'. Viehmeyer (1912: 9) described this species from a single specimen without a locality label ('1 Stück ohne Vaterlandsangabe...'). He did, however, refer to a second specimen in the Forel collection originally from China ('Forel erwähnt die Art aus der Provinz Kien [China]), and obviously accepted China as the true provenance of *P. pyrgops*. In the

introduction to his paper he listed this species as '22. [*Polyrhachis*] *pyrgops* sp. n. China'.

I have examined types of both *P. vigilans* and *P. pyrgops*, including the Chinese specimen from the Forel collection, together with numerous recently collected specimens (Hong Kong, Aberdeen Wood, 5 viii 1994, J. Fellowes; S. China, Guangdong Prov., 27 ix 1995, J. Fellowes). All are remarkably similar. The posteriorly elongated eyes are a prominent feature. I am confident that *P. vigilans* and *P. pyrgops* represent a single biological species.

***Polyrhachis villipes* Fr. Smith, 1857**

Polyrhachis villipes Fr. Smith, 1857: 61. Holotype worker. Type locality: Borneo, Sarawak (A.R. Wallace), OXUM (examined).

Polyrhachis sumatrensis Fr. Smith, 1858: 65, pl. 4, fig. 43. Holotype queen (alate). Type locality: Indonesia, Sumatra (A.R. Wallace), BMNH (examined). Syn. nov.

Polyrhachis striata r. *tritschleri* Forel, 1912: 111 (footnote). Syntype workers. Type locality: Indonesia, Sumatra, Indrapura (Tritschler), MHNG (examined). Syn. nov.

REMARKS. Comparison of the *P. villipes* holotype and *P. striata tritschleri* syntypes shows them to be very similar and undoubtedly conspecific. They are very closely related to *P. striata* Mayr, but, the latter is easily separable by the reticulate-punctate sculpturation of its gaster and the presence of more-or-less distinct lateral carinae on the first gastral segment. In contrast, the gaster in *P. villipes* (including the *P. striata tritschleri* syntypes) is microscopically shagreened and covered with a pile of short appressed pubescence which has a distinct reddish tint on the dorsum.

Subsequent comparison of the holotype of *P. sumatrensis* with the holotype of *P. villipes* and the syntypes of *P. striata tritschleri* was somewhat hindered by the relatively poor condition of the *P. sumatrensis* queen. It is pinned, and has a damaged mesosoma and detached gaster, while the antennae, petiole and both right wings are missing. Nonetheless, the types compare relatively well and differ only in the sculpturation of the occiput, which is more distinctly striate and closely microsculptured in *P. sumatrensis*. This character is, however, accentuated by sculpture associated with the ocelli, which are, of course, not present in the *P. villipes* and *P. striata tritschleri* workers. The striation on their occiputs is somewhat vague and the microsculpture relatively less coarse, yielding a more glossy appearance. Other possibly relevant features, including

the outline of the head, sculpturation and pubescence of the pronotal collar and gaster, and the (mostly black) pilosity, are similar in all three nominal forms. *P. villipes* and *P. striata tritschleri* are clearly synonyms. The above proposed synonymy of *P. sumatrensis* should, however, be considered conditional until worker associated *P. villipes* queens become available for study.

***Polyrhachis inermis* species-group *Polyrhachis carbonaria* Fr. Smith, 1857**

Polyrhachis carbonaria Fr. Smith, 1857: 60. Holotype worker. Type locality: West Malaysia, Melaka (A.R. Wallace), OXUM (examined).

Polyrhachis orsyllus subcarinata Emery, 1900b: 712. Syntype workers. Type locality: Indonesia, Mentawai I., Sipora, Sereinu (E. Modigliani), MCSN (examined). Syn. nov.

Polyrhachis (*Myrma*) *orsyllus* var. *dentulata* Stitz, 1925: 135. Syntype workers. Type locality: Indonesia, Sumatra, Fort de Kock (W. Midcolitz), MNHU (examined). Syn. nov.

Polyrhachis (*Aulacomyrma*) *carbonaria* Smith; Donisthorpe, 1932: 445. Combination in *P. (Aulacomyrma)*.

REMARKS. The holotype of *P. carbonaria* lacks almost all traces of fine appressed silvery pubescence and thus appears more black and shiny than the syntypes of *P. orsyllus subcarinata* and *P. orsyllus dentulata* and other recently collected specimens. The sculpturation is also more distinct in the *P. carbonaria* and *P. orsyllus dentulata* types, notably on the head, where the striae are more shiny than in the *P. orsyllus subcarinata* type. Examples of such sculptural diversity are not, however, uncommon, even in a single series of *P. inermis*-group specimens (e.g. material from Singapore, Bukit Timah, 2 i 1990, R.J. & E. Kohout). The eyes in *P. carbonaria* are fairly convex and exceed the lateral outline of the head in full face view. In contrast, those of *P. orsyllus subcarinata*, *P. orsyllus dentulata* and modern material either do not attain, or at most only marginally exceed the cephalic outline. The relevant types are otherwise very similar. Their few minor differences seem merely to represent infraspecific variation. I am thus confident that *P. carbonaria*, *P. orsyllus subcarinata* and *P. orsyllus dentulata* represent a single biological species.

***Polyrhachis hosei* Donisthorpe, 1942**

Polyrhachis (*Myrma*) *hosei* Donisthorpe, 1942: 708. Syntype workers. Type locality: Borneo, Santubong, i. 1907 (J. Hose), BMNH (examined).

Polyrhachis inermis Fr. Smith; Bolton, 1974: 176. Spurious synonymy.

REMARKS. Bolton (1974: 176) synonymised *P. hosei* with *P. inermis* Fr. Smith. However, following direct comparison of their types I consider them to represent separate biological species. *P. hosei* differs from *P. inermis* (and other species of their group) in a number of details, including its rather flat, somewhat posteriorly truncated eyes (those of *P. inermis* are distinctly convex, with simply rounded posterior margins). The outline of the mesosomal dorsum in *P. hosei* is rather evenly curved, with only slight interruption at the propodeal declivity, while the declivity is abrupt and concave in profile in *P. inermis* and other species of the group, except *P. ritsemai*. The lateral margins of the propodeal dorsum of *P. hosei* terminate posteriorly in short, blunt, up-turned denticles, leaving the dorsal and declivous faces of the propodeum medially uninterrupted. The propodeal dorsum and declivity in other species of the group, including *P. inermis*, are divided by a distinct, transverse ridge. The propodeal declivity in *P. hosei* is laterally delimited by distinct carinae, which run from the bases of the propodeal denticles to the propodeal spiracles.

***Polyrhachis aculeata* species-group**

***Polyrhachis numeria* Fr. Smith, 1861**

Polyrhachis numeria Fr. Smith, 1861: 42, pl. 1, fig. 25. Holotype worker. Type locality: Indonesia, Sulawesi (A.R. Wallace), OXUM (examined).

Polyrhachis (Johnia) schizospina Karavaiev, 1927: 44, fig. 20. Holotype queen. Type locality: Indonesia, Princen Eiland in Sundastrase (Karavaiev #2397) IZAS (examined). Syn. nov.

Polyrhachis schizospina Karavaiev; Hung, 1967: 402. Combination in *P. (Aulacomyrma)*.

REMARKS. Comparison of the *P. numeria* holotype worker, the holotype queen of *P. schizospina*, and additional specimens from BMNH (Andaman Is, 30 v 04, G. Rogers), demonstrates that (apart from the characters identifying full sexuality) they are very similar. Numerous features are essentially identical, including the shape of the head, the posteriorly truncated eyes, the sculpturation being partly covered by rich silvery pubescence, and similarity in the outline of the petiole. There is clear indication that these nominal taxa are conspecific. I therefore consider their types be the worker and queen of a single biological species.

Subgenus *Cyrtomyrma* Forel, 1915

***Polyrhachis doddi* Donisthorpe, 1938**

Polyrhachis (Cyrtomyrma) doddi Donisthorpe, 1938: 263, fig. 13. Syntype workers, queen. Type locality: Australia, Qld (F.P. Dodd), BMNH (examined).

Polyrhachis (Cyrtomyrma) townsvillei Donisthorpe, 1938: 251, fig. 4. Syntype workers, queen, male. Type locality: Australia, Qld, Townsville (F.P. Dodd), BMNH (examined). Syn. nov.

REMARKS. Comparison of the syntypes of both the above nominal species, together with QMBA specimens from the original series of *P. doddi* (Townsville, Qld, 15.2.1902, F.P. Dodd) and abundant modern material clearly demonstrates that these names represent a single biological species. These specimens are virtually identical, except that the colour of their legs is dark to medium reddish-brown in the *P. doddi* types but light yellow in those of *P. townsvillei*. I accept the opinion of Than (1978: 103) that Donisthorpe described both species from a single conspecific series.

***Polyrhachis goramensis* Emery, 1887 stat. nov.**

Polyrhachis rastellata var. *goramensis* Emery, 1887: 239. Syntype workers. Type locality: Indonesia, Goram I. (L.M. D'Albertis), MCSN (examined).

Polyrhachis (Cyrtomyrma) euryalus var. *goramensis* Emery; Donisthorpe, 1938: 260.

Polyrhachis (Cyrtomyrma) obsidiana Karavaiev, 1927: 50, fig. 21. Syntype workers, queens, males. Type locality: Indonesia, Ambon I., Amboina (W. Karavaiev), IZAS, QMBA (examined). Junior primary homonym of *P. obsidiana* Emery, 1921: 21.

Polyrhachis (Cyrtomyrma) coronata Santschi, 1928: 140. Replacement name. Syn. nov.

REMARKS. I have compared syntypes of both the above taxa with material from BMNH (Indonesia, Seram I., Solea, vii 1987, M.C. Day) and am confident that all are conspecific. They are characterised by a moderately impressed promesonotal suture, short, acute propodeal spines, which are sometimes reduced to a pair of short tubercles, and distinctly elongated lateral petiolar spines. *P. goramensis* was originally described as a subspecies ('variety') of *P. rastellata* (Latreille, 1802) and later placed by Donisthorpe (1938: 260) as a subspecies of *P. euryala* Fr. Smith (1863: 16). The characters given above clearly set it well apart from both these species, and I have no hesitation in raising it to specific rank.

***Polyrhachis jurii* Karavaiev, 1935**

Polyrhachis (Cyrtomyrma) jurii Karavaiev, 1935: 116, fig. 30. Holotype worker. Type locality: Cambodia, Ream, Prov. Kampot, Gulf of Siam (K. Davydov #5781), IZAS (examined).

REMARKS. The holotype of *P. jurii* was presumed lost by Than (1978: 13). My search of the Karavaiev collection has, however, unearthed a specimen labelled as the holotype of '*P. (Cyratomyrma) reamensis*', a name apparently never published. It bears two identification labels with that name and two additional tags reading: 'Ream, Cambodge, K. Davidov' and '5781 - Coll. Karawaiew', data identical to those given by Karavaiev for *P. jurii*. This specimen conforms totally with the original description of *P. jurii* and is undoubtedly its 'missing' holotype. '*P. reamensis*' was undoubtedly a manuscript name subsequently changed to *P. jurii*, an action not without precedent in myrmecology (see notes above under *P. hermione*). To avoid future confusion, I have added a red tag to this specimen reading: 'HOLOTYPE *Polyrhachis (Cyratomyrma) jurii* Karavaiev'.

SPECIES INQUIRENDAE

Polyrhachis eudora Fr. Smith, 1860

Polyrhachis eudora Fr. Smith, 1860: 99, pl. 1, fig. 19. Syntype queen, worker. Type locality: Indonesia, Batjan I. (A.R. Wallace), OXUM (queen), BMNH (worker) (both types presumed lost).
Polyrhachis eudora Fr. Smith: Emery, 1925: 183. Combination in *P. (Myrmotherinx)*.

REMARKS. The syntypes of *P. eudora* Fr. Smith cannot be found in the OXUM or BMNH collections and must be considered lost. Donisthorpe (1932: 460) reported their absence from both collections when he wrote: '11. *Polyrhachis eudora* Smith ... Emery [1925] p. 183 = *Polyrhachis (Myrmotherinx) eudora* Smith, ♀. The insect from Oxford does not agree with Smith's description or figure; it is not a *Myrmotherinx*, and is in fact *Polyrhachis (Myrma) proxima* Roger. *P. eudora* is not represented in the B.M. Coll.'

I have examined the queen and worker specimens labelled as *P. eudora* in the OXUM and BMNH collections, and agree with Donisthorpe assignment of them to subgenus *P. (Myrma)*. However, they are not conspecific with *P. proxima* Roger as he suggested, but with *P. decipiens* Roger. I here formally declare *P. eudora* to be a species inquirenda, unable to be confidently identified because of its inadequate original description, and the absence of relevant type material.

Polyrhachis latreillei (Guérin-Ménéville, 1838)

Formica latreillii Guérin-Ménéville, 1838: 205. ?Holotype worker. Type locality: Australia. ?MNHN (type presumed lost).

Polyrhachis latreillii (Guérin-Ménéville); Fr. Smith, 1858: 73. Combination in *Polyrhachis*.

REMARKS. The type of *P. latreillei* cannot be found in MNHN or other examined collections and must be considered lost. Since its description, specimens of a number of different Australian species, including *P. gab* Forel, *P. lata* Emery, *P. senilis* Forel and *P. vermiculosa* Mayr, have been regarded by authors to represent *P. latreillei* and lodged in collections under that name. In fact, the majority of Australian *P. (Chariomyrma)* species fit the original description of *P. latreillei*, and comments made by various authors (e.g., Roger, 1863: 155-158; Emery, 1887: 229) do not help to solve its identity. In the absence of type material the status of *P. latreillei* is soundly ambivalent. I thus formally consider it a species inquirenda.

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NEW DATA ON TYPHLOPID TYPE SPECIMENS FROM QUEENSLAND IN THE COLLECTION OF THE MUSEUM FÜR NATURKUNDE, BERLIN. *Memoirs of the Queensland Museum* 42(2): 532. 1998:- A monographic treatment by Waite (1918) has been the basis for most subsequent studies of Australian typhlopids snakes. However, prior to the initiation of Waite's studies on typhlopids in 1893, some 16 species had been proposed, based on Australian material (Cogger et al., 1983); Waite did not examine type specimens of 15 of these. I have examined the type specimens of Australian typhlopids held in the Museum für Naturkunde der Humboldt-Universität, Berlin (ZMB) and I here present new data on type specimens of four species described by Peters (1867a,b, 1879) from Queensland material.

Ramphotyphlops ligatus (Peters, 1879)

Typhlops ligatus was described from a single specimen (ZMB6231) stated to be from Port Mackay, obtained from the Godeffroy Museum. The holotype (snout-vent length 228mm, tail length 13.5mm, body width 7.7mm) is in good condition, and has 24 midbody scales, 295 dorsal scales, 18 subcaudal scales, nasal cleft from the first supralabial, passing well onto the dorsum of the snout parallel with the rostral, rostral narrow, and snout profile rounded, slightly depressed. The dorsum is dark, and belly pale, with a moderately sharp, linear disjunction between the two shades. It is clearly conspecific with the species to which the name has been consistently applied (Storr, 1981).

Ramphotyphlops unguirostris (Peters, 1867)

Typhlops (Onychocephalus) unguirostris was described from two specimens, stated to be from Roekhampton, in the collection of C. Godeffroy (Peters, 1867a). The larger specimen (length 450mm, width 8.7mm) was noted to have 24 midbody scales, and the smaller specimen (length 135mm, width 3mm) had 18 midbody scales. McDowell (1974), nominated the larger as lectotype, and followed Boulenger (1889) in identifying the smaller specimen as *Ramphotyphlops affinis*. Neither author indicated that they had examined Peters' types. The two type specimens are registered as ZMB5884 (Cogger et al., 1983). Both are in good condition.

The lectotype (snout-vent length 432mm, tail length 6mm) is typical of the species currently recognised as *R. unguirostris*. It has 24 midbody scales, 543 dorsal scales, 9 subcaudal scales, and the nasal cleft from the first supralabial, extending just beyond the nostril. The rostral is broad, but has a noticeably narrowed posterior extremity, and in this respect does not agree with the illustration by Peters (1867). The paralectotype (snout-vent length 128mm, tail length 4mm) has 18 midbody scales, 423 dorsal scales, 16 subcaudal scales, the nasal cleft from the second supralabial, and is conspecific with the holotype of *Ramphotyphlops affinis*, confirming Boulenger's identification.

Typhlops curvirostris Peters, 1879 was described from a single specimen (ZMB7525), stated to be from Port Bowen, obtained from the Godeffroy Museum. The original registration entry for this specimen gives the locality as Bowen, Port Denison. The holotype is now in very poor condition, with the body breaking apart into soft fragile segments, held together only by the stratum corneum of the epidermis. I was unable to accurately measure the specimen, but it has snout-vent length approximately 292mm (Peters gives 300.5mm), 24

midbody scales, approximately 536 dorsal scales, 9 subcaudal scales, and the nasal cleft from the first supralabial. The protrusive, slightly hooked snout is similar to that of the lectotype of *unguirostris*, and the two types are certainly conspecific, supporting Waite's synonymy of the two species.

Ramphotyphlops wiedii (Peters, 1867)

Typhlops wiedii was described from material from Brisbane (Peters, 1867b). Only one set of measurements was provided in the type description (snout-vent length 241mm, tail length 4mm, body width 4.3mm). Only one specimen in the ZMB collection identified by this name has the locality Brisbane (ZMB5845), and is identified in the registers as the holotype. This specimen (snout-vent length 228mm, tail length 4mm, body width 4.0mm) is typical of the species to which the name has been subsequently applied (Waite, 1918; Shea, 1995), with 20 midbody scales, 400 dorsal scales, 10 subcaudal scales, nasal cleft from the second supralabial, extending well onto the head dorsum, and failing to completely divide the nasal. The snout is rounded in profile and slightly blunt when viewed from above.

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TURINIA PAGEI (POWRIE): A NEW RECONSTRUCTION OF THE SOFT ORGANS OF THE CEPHALOTHORAX

L.I. NOVITSKAYA AND S. TURNER

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The possible structure and mutual arrangement of some of the inner soft organs of *Turinia pagei* (Powrie) including the brain, pineal organ, olfactory sacs, semicircular canals, and branchial sacs are reconstructed. The details of morphology of departments of the brain and organisation of the branchial system are analysed. We interpret *T. pagei* as having paired nasal sacs and a telencephalon possessing well-developed olfactory tracts. Traces of the labyrinth are present at the level of the second and third gill pouches. In both these characters *T. pagei* was similar to heterostracans and early gnathostomes (placoderms, chondrichthyans). On the basis of a suite of characters including new data on the inner organisation of *Turinia* and *Lanarkia*, thelodonts represent a monophyletic group phylogenetically nearest to, and thus should be considered as the sister group of the gnathostomes. □ *Silurian, Devonian, agnathans, Thelodonti, brain, nasal sacs, stomach.*

Larissa I. Novitskaya, Paleontological Institute of the Russian Academy of Sciences, Profsoyuznaya 123, Moscow 117647, Russia; Susan Turner, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 27 March 1996.

Thelodonts are extinct agnathan fishes (Late Ordovician-Late Devonian [early Frasnian]) which possess an exoskeleton of discrete dentinal scales with a base of acellular bonelike tissue (aspidin) which is capable of growth, and the production of simple to complex anchoring devices. The squamation is subdivided into several specialised scale areas. These characters were used by Turner (1991) to define the Thelodonti as a monophyletic group. Thelodonts are known mainly from isolated scales which are found abundantly in many deposits around the world. Taxa known from articulated specimens are few (although the number of specimens is large), preserved only in exceptional environments from the Silurian of Scotland, Norway, Canada and Estonia, and from the Early Devonian of Britain and Canada (Turner, 1976, 1982; Wilson & Caldwell, 1993; Caldwell & Wilson, 1995). Recent studies on the general morphology, squamation, and internal organisation of the thelodonts are providing new information on the nature of these fossil fishes, leading to diverse interpretations of the structures and consequently, different ideas about their relationships, some regarding them as monophyletic (e.g., Turner, 1991; Turner & van der Bruggen, 1993; van der Bruggen, 1993) and others as paraphyletic (van der Bruggen & Janvier, 1993; Wilson & Caldwell, 1993; Caldwell & Wilson, 1995). Closer scrutiny of the squamation and internal morphology seems to us to support the impressions of many early workers that

thelodonts are most like chondrichthyans, generally called 'sharks' in the older literature. This hypothesis was reiterated by Stetson (1931), supported by Novitskaya (1983, p. 148), and expanded on by Turner (1985, 1991). Most of these studies have been done on a wealth of old and new specimens of *Loganellia scotica* (Traquair), *Shielia taiti* (Stetson) and *Lanarkia* species from the classic Silurian Lagerstätte in the Southern Uplands, Scotland, which have now been newly described by Märss & Ritchie (1998), who also find evidence for gnathostome characters in the Silurian thelodonts. A suite of fossils from Arctic Canada, the so-called 'fork-tailed' thelodonts, is providing new insights into the range of variation in thelodont morphology (Wilson & Caldwell, 1993; Caldwell & Wilson, 1995) but these fossils have not yet been fully described and will not be considered here in detail.

In late 1994, the authors had the opportunity to review together thelodont collections held at the Queensland Museum and the data from new specimens. Among the studied materials was the cast of the holotype of *Turinia pagei* (Powrie) the original of which exhibits clearly the traces of soft inner organs on its surface (see e.g., Turner 1982, pl. 97). In addition, although not pointed out previously, the rounded clay mass just ventral to the cephalothorax is interpreted here as remains of stomach contents in this thelodont. The presence of a true stomach in thelodonts has only

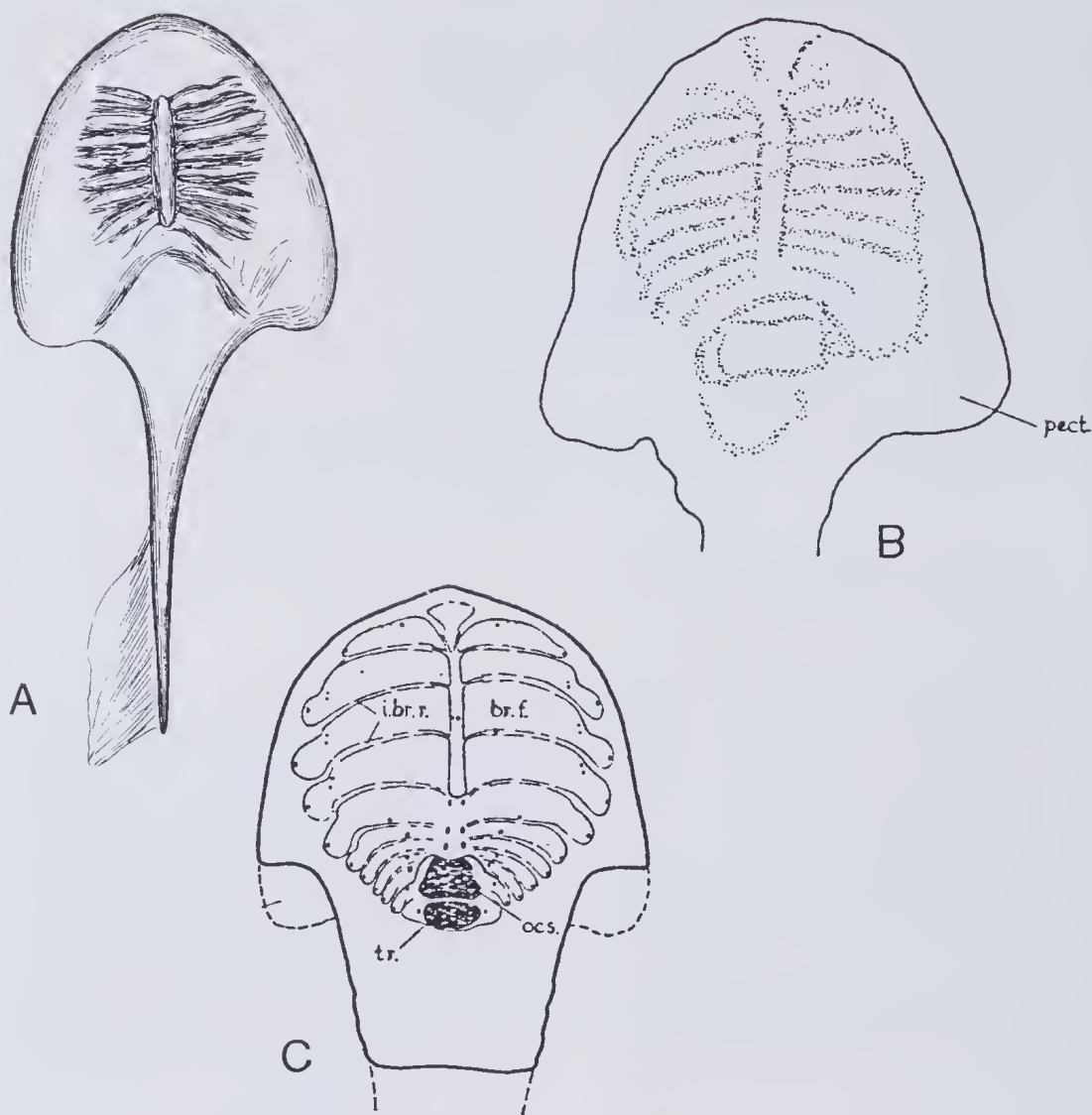


FIG. 1. Comparison of two former different interpretations of the holotype of *Turinia pagei*: A, Powrie, 1870, as 'ventral view'; B, Westoll 1945, as a 'larval cephalaspid' with his drawing of the outline of the cephalothorax 'after Traquair, 1899a'; compared with C, a cephalaspid based on Stensiö (1927) figures of *Kiaeraspis*, showing conformation of roof of branchial cavity etc.; Westoll figured 'br f'=branchial fossa, 'i br r'=interbranchial ridge, oes=oesophagus, pect=pectoral fin, tr=opening for truncus arteriosus.

recently been verified by Wilson & Caldwell (1993) and van der Bruggen (1994).

Turinia pagei was discovered and first described by Powrie (1870, Fig. 1a); the specimen is preserved in fine-grained Lower Devonian sandstone from Turin Hill, Forfar, Scotland. We concentrate on this example because it is one of the few complete specimens of a Devonian thelodont and because, unlike other complete thelodonts mentioned above, this specimen is

preserved as a natural mould in three-dimensions with friable remnants and impressions of scales present. The range of scale variation can be compared with that of other articulated but incomplete specimens of *T. pagei* (e.g., Traquair, 1899; Ørvig, 1969; Turner in Allen et al., 1968) and with isolated scales from numerous marine and marginal or non-marine localities from around the former Old Red Sandstone continent (e.g., Gross, 1967; Turner, 1973; Karatajute-Talimaa, 1978).

TABLE 1. Differences of interpretation of the holotype of *Turinia pagei* in earlier literature compared with the present study. Abbreviations: ant.=anterior; cart.=cartilaginous; d=dorsal; interbr.=interbranchial; longit.=longitudinal; oesoph.=oesophageal; pters.=pteraspid; v= ventral.

Author	Identity	View	Mouth	Eyes	Nasal sacs	Longit. ridge	Brain	Otic	Branch-ial sacs	Branch-ial arches	Branch-ial openings	Gut	Pectoral appendage	Tail	Other
Powrie 1870	own family ray-like	v	ant.	?	?	branch-ial skeleton	-	-	-	7/8 'exposed'	-	-	fins	'entirely below'	no ventral, anal or dorsal fins
Lankester 1870	early shark/ ray	v?	-	-	-	-	-	-	-	-	-	-	-	-	
Traquair 1899	<i>Thelodus</i> Heterostraci shark origin	d	?	?			-	-	-	8 cart. skeleton	-	-	lateral fin-folds	heterocercal broken off	no ventral, anal or dorsal fins
Kemna 1903	<i>Thelodus</i>	d	-	-	-	-	-	-	8 'poches' OR	8 arcs?	none		fins		branch-ial skeleton
Stensiö 1927	Heterostraci	d	cf. pters.	?small cf. pters.	cf. pters.	occipital region	'solid' endocranium	not shown cf. pters.	mesodermal sacs 7+	undivided interbr. ridges	no sign	oesoph. foramen	not certain		cartilage perichondral bone (thin)
Westoll 1945	larval cephalaspid	d		none		aortic groove cf. <i>Kiaeraspis</i>				paired pockets	interbr. ridges				roof branch-ial chamber
Stensiö 1958/ 1964	Heterostraci	d		echancure			occipital region endocranium	labyrinth	8 'fosses'	visceral arches interbr. ridges 1-10? shows 9	8 extra-branch-ial atria	oesoph. foramen conduit for branch-ial vessels			hyoid arch mandibular
This Paper	thelodont basal gnathostome	d	sub-terminal	?	paired	see brain	endocast present with pineal	trace paired between br. 2/3	7 (8?)	long, narrow	separate ?	stomach present	fins	uncertain hypocercal	perichondral bone implied

The traces of the endoskeleton and various inner organs are either rarely preserved in thelodonts or, because of the nature of their preservation, are difficult to interpret. Despite being known for over 160 years, the group remains enigmatic and was until recently poorly characterised. Turner (1991) proposed the monophyly of the Thelodonti based on features of gross and scale morphology (see also Forey, 1984). Ideas about the inner organisation of thelodonts have been mostly reduced to creation of very generalised schemes which had as their foundation information from only a few specimens. Various interpretations of the preserved structures of the holotype and only complete specimen of *T. pagei* have been given (e.g., Powrie, 1870; Traquair, 1899; 1906; Westoll, 1945; Stensiö, 1927, 1964; Fig. 1, Table 1). The present study of the cast of the holotype *T. pagei* concludes that the arrangement of ridges and hollows shown on the cephalothorax can be interpreted as various endoskeletal features and soft organs allowing a

new reconstruction (Fig. 2a). The new data from the holotype of *T. pagei* concern mainly the brain, nasal sacs and branchial system. This information diminishes the gaps in our knowledge of the internal organisation of the thelodonts. We thus regard the latter as being significant for the further study of the problem of phylogenetic relationships of the ancient agnathan and gnathostome vertebrates.

The first turiniid thelodont was found in the classic Old Red Sandstone area of the northern hemisphere in deposits which until recently were thought to be non-marine sediments. The type specimen, '*Cephalopterus*' *pagei*, was discovered by Powrie in 1870 in the Lower Devonian of Turin Hill, eastern Scotland. That year both Powrie and Lankester considered that the holotype was preserved in ventral view; Powrie interpreted seven or eight pairs of 'exposed' branchial arches and thought it 'strangely allied to the modern Rays' (see Powrie's restoration in Fig. 1a); Lankester (1870) noted the resemblance to the

ventral surface of a cephalaspid but thought that the fossil was an early representative of the sharks and rays. Traquair (1899) was the first to seriously consider the significance of *T. pagei* in the light of new Silurian thelodonts he was also studying. He had renamed the holotype *T.* (Turner, 1976) and, in 1899, gave a full description of the specimen, reverting to the type genus *Thelodus*. He noted the absence of jaws and teeth and deduced that the arrangement of ridges and grooves was simply an indication of the presence of a cartilaginous branchial skeleton. Contrary to Powrie he did not believe that the branchial arches were exposed but, because he believed that the thelodont tail was heterocercal, he interpreted the fossil as preserved in dorsal view exhibiting eight pairs of cartilaginous arches, the last pair tending backwards in a reversed V-shape. Kemna (1903) went on to study *T. pagei* by comparison with other thelodonts ('coelolepids') known at the beginning of the 20th century. He surveyed the history of *T. pagei* and noted the differences of opinion on the determination of the visible side of the holotype. Kemna, following Traquair's (1899) opinion on the caudal fin, interpreted it as the dorsal side. While giving arguments pro and contra the interpretation of the branchial structures as visceral or branchial arches, he left the question open for further discussion. Subsequently, there have been several interpretations of the morphology of *T. pagei* and its systematic position compared to other thelodonts and in the overall interrelationships of agnathans (e.g., Westoll, 1945; Stensiö, 1927, 1964; Karatajute-Talimaa, 1978; Turner, 1982, 1991; Janvier, 1996). Information on the soft organs, however, is almost absent from the preceding literature. A brief interpretation of some of them was given by Stensiö (1958, 1964). Stensiö considered *T. pagei* as separate from other thelodonts; he placed it within the Heterostraci based on the configuration of the branchiae and the possession of an endocranium. Westoll (1945), however, preferred to return to the similarity to cephalaspids, notably *Kiaeraspis* (Fig. 1b, c). However, in considering the Turiniidae, Stensiö gave his main attention to the exoskeleton, which is not the subject of this paper. Only on the plate illustrating the holotype did he interpret the morphology of the branchial apparatus (e.g., Stensiö 1964, fig. 89) where he distinguished at least eight pairs of branchial sacs. His hypothesis will be considered further below in connection with analysis of questions remaining in the reconstruction of the inner organs of *T. pagei*.

As will be apparent in our description of the soft parts which follows we now interpret the cephalothorax of the holotype as being preserved in dorsal view because of the imprints of the olfactory tracts and aspects of the brain.

DESCRIPTION

The type specimen of *T. pagei* is the natural cast of an intact animal not deformed in any way. The counterpart apparently was not found. Table 2 displays measurements of *T. pagei*. The total length was taken from the middle of the anterior border of the head to the (broken) end of the lower lobe of the caudal fin; the maximum width is across on the level of postero-lateral points of the lateral brim. The caudal peduncle was taken across the narrowest point in front of the tail. As preserved, the anterior part of the body is relatively flat. The well-developed lateral brim (of the pectoral fin) starts just posterior to a slight bulge in the outline of the specimen, interpreted here as the possible position of the orbit, shown in Fig. 2a with a dashed line. Alternatively, the eyes might be placed directly on the antero-lateral border of the cephalothorax in a more lateral position and thus, as Traquair (1899) noted, they are not preserved. The pectoral extension (variously called the 'flap' or 'fin' in the literature; here we use the term 'fin') thus starts a little in front of the first pair of raised ridges or branchial structures, which we interpret as branchial sacs (see below), becoming larger in a caudal direction. This lateral rim of the fin is flatter than the raised central portion of the large cephalothorax. The cephalothorax in thelodonts usually comprises around one-quarter to one-third of total body length (Turner, 1991); at least the latter in the case of *T. pagei*. The external border of the lateral brim is rounded. The postero-lateral lobes of the fin have a rounded-triangular form. Behind the widest part of the lateral brim and cephalothorax the body tapers suddenly to a quite narrow peduncle. On the type specimen in between the lateral brim (distal pectoral lobes of the fin) at the posterior part of the cephalothorax can be seen a large rounded mass preserved as a darker clay-like sediment. The configuration of the median fins is not clear but there is a probable anal fin preserved on the right hand side of the specimen. The upper lobe of the tail fin is short, the lower lobe is well formed and elongated but not complete as the rock is broken (or trimmed) at this point. These lobes are apparently rounded. They are connected by a series of undulations which might represent a tail web. The tail fin is apparently hypocercal.

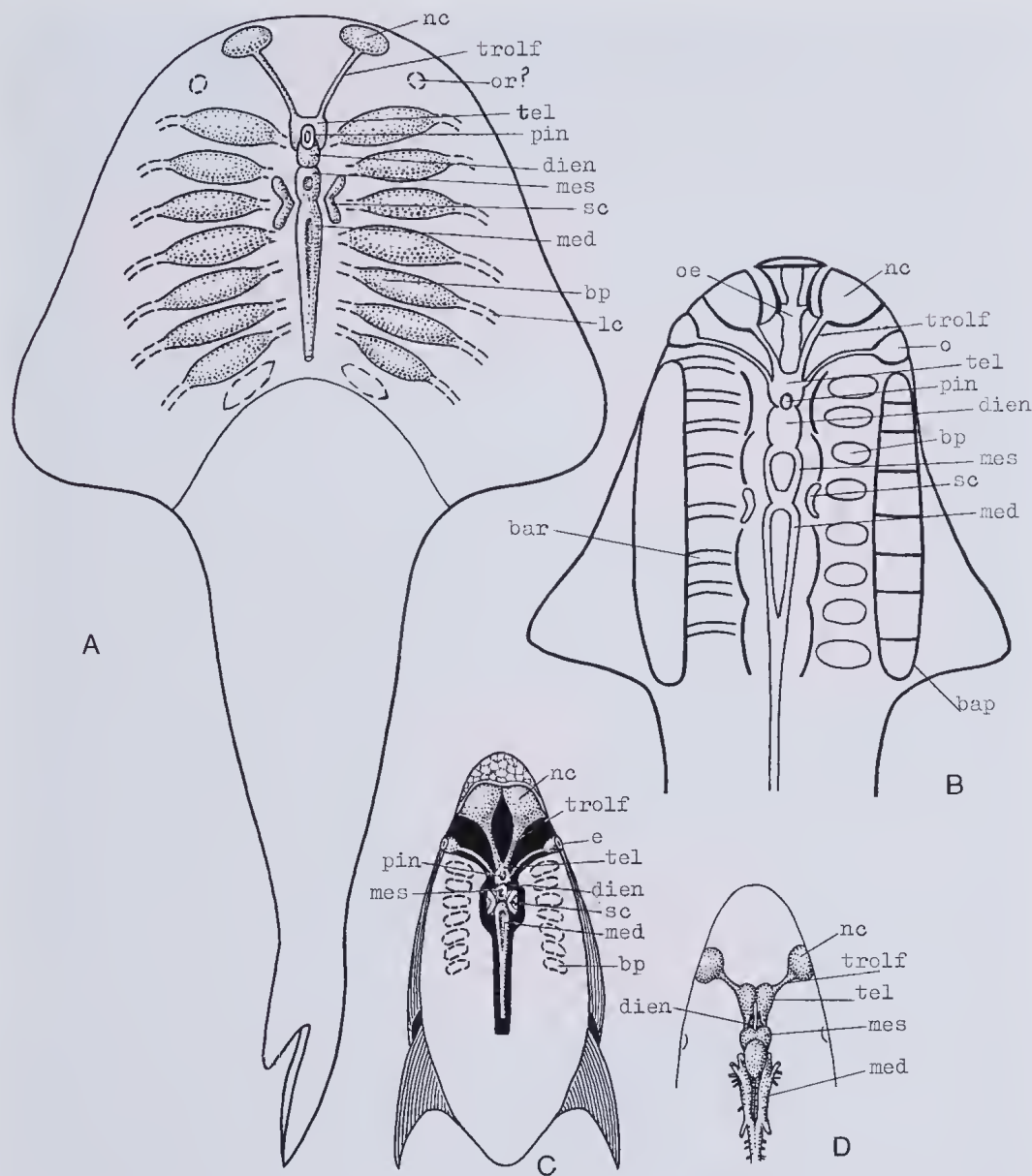


FIG. 2. Diagrammatic representation of the inner organisation of thelodonts, heterostracans and sharks. A, stylised drawing of main features of *Turinia pagei* (Powrie) based on the cast of the holotype, National Museums of Scotland RSM 1891. 92. 133. B, *Lanarkia horrida* (from Turner & van der Bruggen, 1993). C, pteraspid heterostracan of *Podolaspis* type (modified from Novitskaya, 1993). D, shark, *Squalus acanthias* (simplified from Marinelli & Strenger, 1959). Abbreviations: bap=branchial apparatus or row with branchial compartments; bar=possible position of visceral arch; bp=possible branchial pouch; dien=diencephalon; lc=lateral branchial canal; med=medulla (myelencephalon); mes=mesencephalon; nc=nasal capsule; oe=oesophagus; or=orbit; pin=pineal macula (probable position in thelodonts: A, B); sc=location of semicircular canals (uncertain in thelodonts: A, B); tel=telencephalon; trolf=olfactory tracts.

The traces of some soft organs are clearly preserved on the dorsal side of the holotype. These are discussed below.

THE BRAIN. In his explanations of inner structures of *T. pagei*, Stensiö (1964, p. 272, fig. 89: 'r.oc') noted the existence of a thickening formed

TABLE 2. Main measurements of *Turinia pagei* - RSM 1891.92.133.

Character measured	Measurement (mm)	Ratio
medial total length (mtl)	320	
cephalothorax length (cl)	120	mtl/cl = 2.6'
maximum width (mw)	155	mtl/mw = approx. 2
length of pineal organ (po)	5	
width of po	1-1.5	
length of pineal macula (pm)	8-9	
width of pm	7	
width at level of po	95	mw/po = 1.6
width of caudal peduncle (cp)	30	
length of lower caudal lobe (ll)	45	mtl/ll = approx. 7.5
maximum width of lateral brim (lb)		mw/lb = 5

by the occipital region of the endocranium. This thickening continues forward into the otic region of endocranium. Our study of the cast of the holotype shows that the traces of the compartments of the brain can be distinguished in this thickening. Here we propose the following interpretation of the brain.

A pair of shallow but clear grooves is visible on the anterior part of the head. They diverge from the region situated in front of the pineal organ (see below), continue in the direction of the anterior border of the head and terminate not far from it (Fig. 2a, Fig. 3, trolf). We equate these grooves with the tracti olfactorii of modern sharks and other diplorhinal animals, for example, *Lanarkia* (Turner & van den Bruggen, 1993; Fig. 2b), and the Palaeozoic heterostracans (Fig. 2c), by comparison with their position relative to the pineal organ and the anterior border of the head, and by their length. The position of anterior ends of olfactory tracts indicates the place of the paired nasal sacs which were situated near the anterior border of the head on either side of the presumed just ventral mouth opening. The bulbous shape of the nasal sacs is apparent. The telencephalon is not distinguishable but it is possible to estimate its place indirectly, based on the position of the pineal organ and, therefore, from the position of the diencephalon. The pineal organ was situated on a level of the anterior pair of the branchial sacs. Its trace has the appearance of elongated oval pit bordered by a low convex border visible on the surface of the cast. The dimensions of the pit and pineal macula (including convex border) are shown in Table 2. The position of pineal macula indicates that of the diencephalon

since, as far as it is known, the pineal organ in agnathans is always associated with the diencephalon. The preserved surface shown on the cast becomes somewhat lower in front of the diencephalon. In all probability the telencephalon in *T. pagei* was placed in the region of this depression, that is, the upper surface of telencephalon was lower than the upper surface of diencephalon. Alternatively, the depression might be the back of the mesencephalon which is often opposite gill pouch #1 in gnathostomes (Mallatt, pers. comm.). The posterior limit of diencephalon is marked by a weak groove behind the pineal macula. Thus the posterior edge of the diencephalon is placed approximately on the level between the first and the second pairs of branchial sacs.

The natural casts of the mesencephalon and myelencephalon or their endocranial casts are visible on the holotype of *T. pagei* behind the diencephalon although the limit between the mesencephalon and myelencephalon is poorly distinguished. The junction of mesencephalon and myelencephalon was on a level approximately between the second and third pairs of branchial sacs. Further back the cast of myelencephalon is seen distinctly, extending back as far as the posterior branchial region. The traces of anterior and posterior semicircular canals are seen on the level of second and third branchial sacs (Fig. 3, sc. (lab.)), but the imprints of the canals are not perfectly clear. The possible position of the labyrinth in the same place was also indicated by Stensiö (1964, fig. 89, 'lab?') although our numeration of the branchial sacs does not coincide with his.

BRANCHIAL STRUCTURE. The casts of the branchial sacs are clearly visible on the holotype of *T. pagei*. The branchial sacs were large and situated overall transversally. They diminished in size in a caudal direction (Figs 3-4). The branchial sacs are situated near to one another. Seven pairs of them are clearly distinguishable. The presence of the eighth most posterior pair is not definite but the possible position is indicated in Fig. 2a. The anterior pair of branchial sacs is the largest, oriented transversally and obliquely; their lateral ends are directed forward. The orientation of sacs changes from anterior to posterior: the lateral ends of posterior branchial sacs are directed obliquely and back.

Unfortunately, the preservation of material still does not allow us to answer the question of how the branchial sacs of *T. pagei* opened to the outside. We still cannot determine whether they had separate branchial openings or individual canals

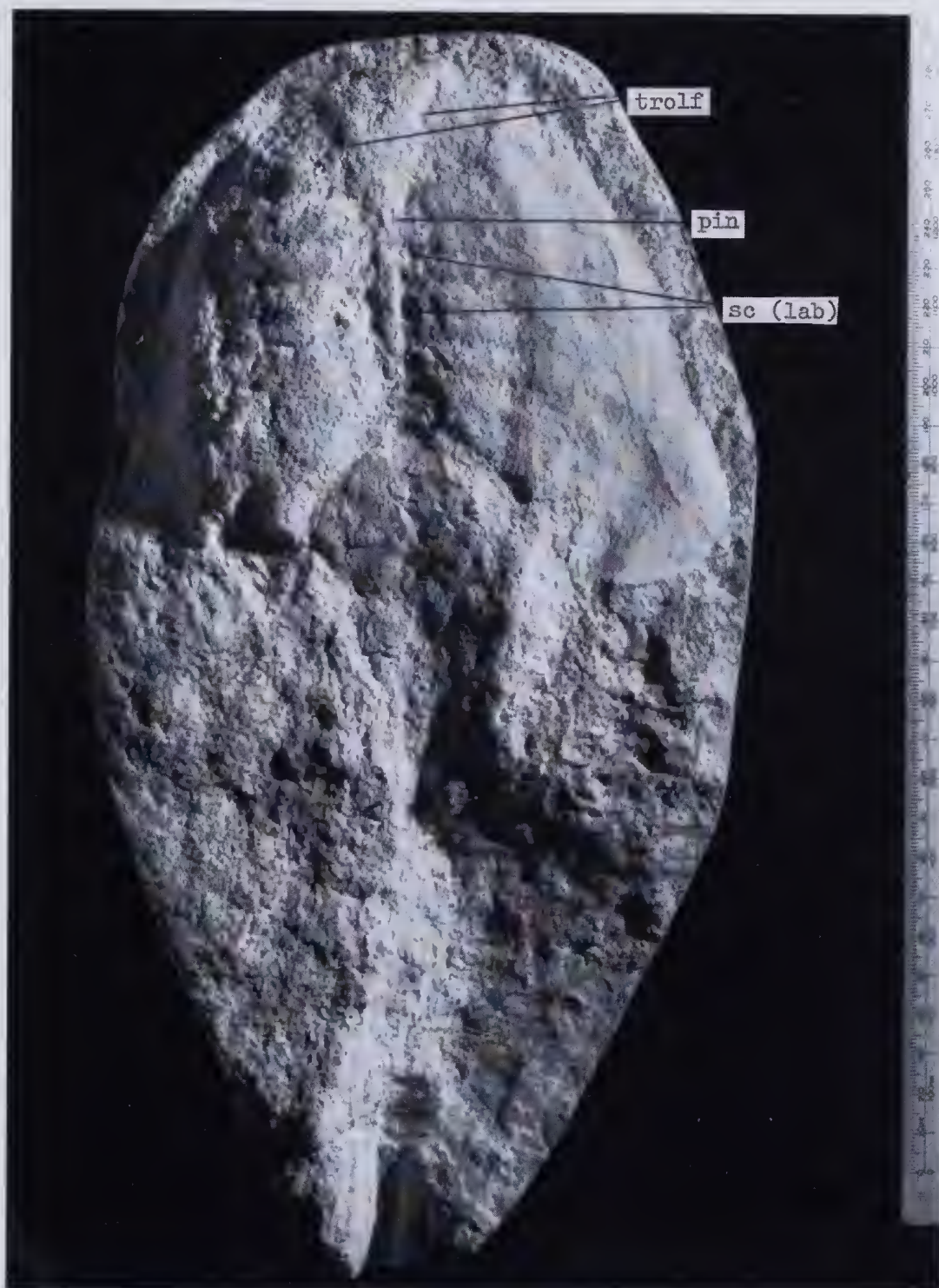


FIG. 3. Photograph of the cast of the holotype of *Turinia pagei* (Powrie) exhibiting the position of olfactory tracts (trolf), brain, pineal organ (pin), possible semicircular canals (sc (lab)). Impressions of brain stem and branchial sacs can be seen. Holotype (RSM1891.92.133; Museum of Scotland, Edinburgh) from the Early Devonian (Lochkovian) Old Red Sandstone of Turin Hill, Forfar (Scotland).

leading out to a common atrial canal. The slight thickening which is seen on the lateral brim of *T. pagei* was interpreted as the anterior branchial canal by Stensiö (1964, 'conduit branchial antérieur'). Such an interpretation sat well with his idea of *T. pagei* being an heterostracan. Our investigations show, however, that this canal was not continuous but consisted of short separated segments (Fig. 4, icbr). The curved imprints, which were explained by Stensiö (1964, fig. 89) as extrabranchial atria, are seen to be more lateral relative to each branchial sac. Similar imprints or natural casts can be seen in many heterostracans (e.g., Novitskaya, 1983). In all probability these imprints represent the traces of individual branchial canals leading from the branchial sacs. In some thelodonts, for example in *Phlebolepis elegans* (Ritchie, 1968), and the recently discovered fork-tailed thelodonts (Wilson & Caldwell, 1993), the branchial sacs each opened out separately.

As already noted, the casts of the branchial sacs in *T. pagei* are situated near to one another. If this state was not due to posthumous alteration such as contraction, the branchial arcs (arches) appear to have been very long and narrow and subequal in size. The first visceral arch was apparently situated immediately behind the eye. In *T. pagei*, the posterior arches were shorter than the more anterior ones. As with the pharyngeal arrangement in modern primitive sharks, this pattern matches well with the extrabranchial cartilages of sharks (Mallatt, pers. comm. 1996).

DISCUSSION

On the whole, the organisation of the visceral system in *T. pagei* has overall similarity to that of heterostracans and some other agnathans (Gagnier, 1995). Such common traits are observed in the presence of a few branchial sacs, in their form and disposition, in the presence of individual (for each sac) lateral canals and in the simple structure of cartilaginous non-differentiated branchial arches. Whether similar characters were inherent also in the most archaic vertebrates is still in debate. To a certain degree the finds of Ordovician vertebrates in Australia (*Arandaspis*: Ritchie & Gilbert-Tomlinson, 1977) confirm this. Some current analyses have led to the conclusion that cephalaspids, with their highly specialised morphology are the sister-group of gnathostomes and that thelodonts are paraphyletic (e.g., Forey & Janvier, 1994). However, we consider that the *T.* pattern seems to show what some regard as the primitive gnathostome condition (e.g., Novit-

skaya, 1983; Gagnier, 1995). The arrangement is comparable with living early gnathostome embryos with first gill arch and pouch just behind the eye, second arch (the hyoidean) just in front of the otic capsule and so on (e.g., Mallatt, 1996). Thus, the primitive vertebrate pattern might be a high number of paired branchial structures, as in galeaspids and some Ordovician forms (Gagnier, 1995; Janvier, 1996). A small number of eight paired branchial structures, as seen in *Turinia*, which might functionally have been only seven pairs; this recalls the suggested pre-gnathostome pattern (Mallatt, 1996) which is close to that seen in modern primitive chondrichthyans such as *Heptanchias* and *Chlamydoselachus*.

Consideration of the morphology of *T. pagei* indicates the internal organisation of one thelodont, although to understand some organs, principally the branchial system, we need more precise data. At the same time the new interpretation makes it possible to compare *T. pagei* with *Lanarkia horrida*, another thelodont in which the soft organs have recently been reconstructed on the basis of good new material (Turner & van der Bruggen, 1993). Comparison shows that *Turinia* and *Lanarkia* were similar in the main pattern of their inner organisation. The presence of possible well developed long olfactory tracts and paired, separate large nasal sacs of gnathostome type in both thelodonts are the most significant common characters. From our study of *T. pagei*, it is clear that the reconstruction of the labyrinth in *L. horrida* was probably placed too far back by Turner and van den Bruggen (1993; the brain configuration needs to be slightly altered to abut the semicircular canals with the level of the 2nd and 3rd gill pouches. However, as shown on the comparative scheme (Fig. 2), both thelodonts are similar in the characteristics of the cephalothorax to heterostracans and basal gnathostomes. The same position of the telencephalon in relation to the upper surface of diencephalon is found in heterostracans (Novitskaya, 1974, 1983) and lampreys (Marinelli & Strenger, 1954; Fontaine, 1958). The pineal organ was situated on a level of the anterior pair of the branchial sacs, as in heterostracans (Novitskaya, 1983, fig. 64). The posterior limit of diencephalon occupies a similar position in heterostracans, e.g., *Poraspis pompeckji* (Novitskaya, 1983, pl. 4, figs 2, 3). Because the labyrinth is not clearly seen, it is possible that the semicircular canals were placed somewhat deeper in the endoskeleton in *T. pagei* than in some other early vertebrates. In heterostracans, for example, the semicircular canals retain very clear

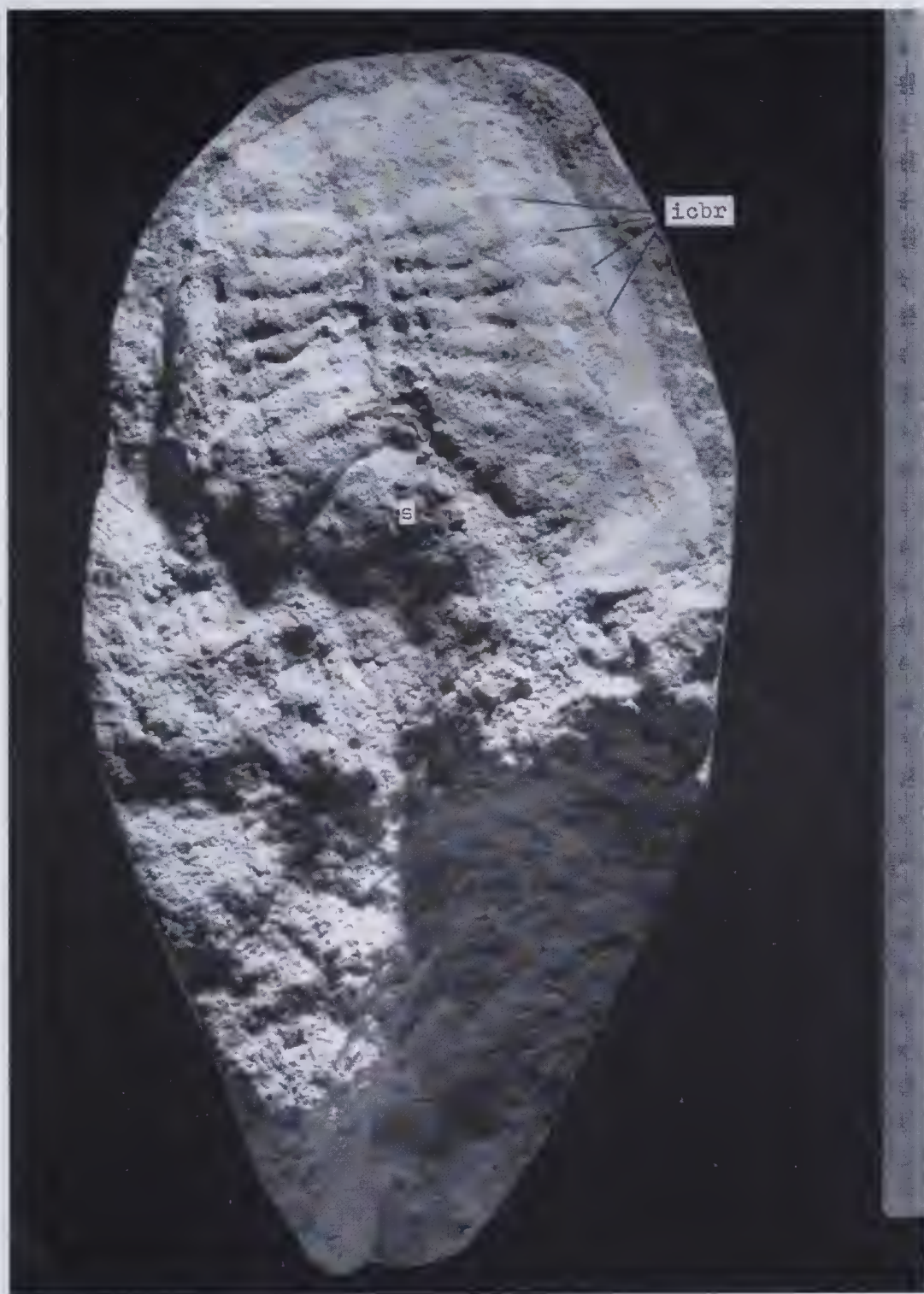


FIG. 4. Photograph of the cast of the holotype of *Turinia pagei* (Powrie). Different direction of light makes the traces of branchial apparatus clearer: icbr=individual branchial canals; s=position of stomach contents.

traces which can be seen in cyathaspids such as *P. pompeckji* (Brotzen), *P. cylindrica* Kiaer, *Komalaspis della nitida* (Kiaer) (e.g., Stensiö, 1964, figs 81A,B-82A,B; Novitskaya, 1983, pl. IV, figs 2, 3).

The comparison of thelodonts and heterostracans shows that the visceral arch situated immediately behind the eye in *T. pagei* corresponds to the mandibular arch of heterostracans. This structure was homologised to that of lower gnathostomes (using a shark embryo) by Novitskaya (1983). The second arch is compared to the hyoidean in sharks, the following to the first branchial arch and so on (Novitskaya 1983, fig. 71, p.133). The similarity of thelodonts, heterostracans and basal gnathostomes in the disposition of the named visceral arches and the large nasal sacs, leads us to consider the visceral skeleton as homologous in all three groups.

The presence of these characters in the morphology of the named groups and the evidence from the holotype of *T. pagei* testify that a common nasohypophysial duct of cephalaspid type did not form in their ontogenesis (contra van der Bruggen & Janvier, 1993). Furthermore, the type of ontogenesis (development) in thelodonts was fundamentally similar to that of heterostracans and basal gnathostomes. The method of reconstructing the developmental type of an agnathan on the basis of their morphology was earlier demonstrated by Novitskaya & Karatajute-Talimaa (1989) and Novitskaya (1993).

SUMMARY

The organisation of the visceral skeleton, the number of branchial sacs (at least seven or at most eight pairs), and the position of the anterior pair relative to the pineal organ, are similar in *Turinia* and *Lanarkia*. The characters noted here, as with some others concerning the internal morphology and the exoskeleton (Novitskaya, 1983; Turner, 1991), are similar also in these thelodonts and in heterostracans. At the same time the presence of external openings of branchial sacs ventral to the pectoral fin-lobes, now known in some thelodonts, separates them from the specialised heterostracans which possessed a common removal branchial canal with one common external opening or atrium.

The mouth in *T. pagei* was apparently anterior and just ventral, flanked by paired nasal capsules. No evidence for a nasohypophysial organ is seen. The branchial row which began just behind the eyes, was relatively foreshortened with openings in all probability ventral to the pectoral fins as

known in *Phlebolepis elegans* and *Loganellia scotica*.

In *T. pagei* the morphology of the divisions of the brain (diencephalon, mesencephalon, myelencephalon) is simple and similar to that in such groups of vertebrates as lampreys, heterostracans, and arthrodires (e.g., Novitskaya, 1993). In the morphology and disposition of these brain compartments, *T. pagei* is generally similar to *Lanarkia*. The brain is homologous with that in heterostracans and in lower gnathostomes (e.g., chondrichthyans). The pineal organ was preserved but there was no nasohypophysial organ. The paired semi-circular canals are placed in the region of the branchiae 2 and 3. Other characters such as the presence of specialised denticles lining the mouth and pharyngeal region, morphological style and complexity of the external squamation, presence of a stomach (see e.g., Fig. 4, s), indicate close similarity between thelodonts and chondrichthyans.

In agreement with the above-mentioned similarities between thelodonts and lower gnathostomes (in morphology of olfactory organ, telencephalon, in apparent absence of a common nasohypophysial organ) we believe that thelodonts shared a similar type of ontogenesis (see Novitskaya & Karatajute-Talimaa, 1989). This, and the presence of external removal openings for each pair of branchial sacs, seen in some thelodonts (but not here in the holotype of *T. pagei*), provides the basis for considering them as the group most similar to basal gnathostomes in the main traits of organisation. Among Palaeozoic agnathans the thelodonts are thus considered to be the group phylogenetically nearest to gnathostomes (chondrichthyan fishes). This idea has been considered previously by both authors on the basis of other material and other characters (Novitskaya, 1983; Turner, 1991). A recent cladistic analysis of early vertebrates arrived at a similar conclusion that places thelodonts as the sister group of gnathostomes (Gagnier, 1995). The new data on the internal organisation of *T. pagei* presents evidence supporting this hypothesis.

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OSTEOLOGY OF A SPERM WHALE *PHYSETER MACROCEPHALUS* (LINNAEUS) FROM CENTRAL QUEENSLAND

R.A. PATERSON, H.A. JANETZKI AND S.C. WILLIAMS

Paterson, R.A., Janetzki, H.A. & Williams, S.C. 1998 06 29: Osteology of a sperm whale *Physeter macrocephalus* (Linnaeus) from central Queensland. *Memoirs of the Queensland Museum* 42(2): 545-553. Brisbane. ISSN 0079-8835.

The osteology of a subadult, male sperm whale (12.2m) collected from the central Queensland coast is described. Its mean vertebral length (MVL) is compared with a male specimen from the Japanese coast. There is no appreciable difference in vertebral proportions, particularly in the caudal region, between these specimens from the Northern and Southern Hemispheres. □
Sperm whale, Physeter macrocephalus, osteology.

R.A. Paterson, H.A. Janetzki and S.C. Williams, *Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 1 December 1997.*

A male sperm whale (12.2m) stranded at Joskeleigh Beach via Keppel Sands (150°48'E, 23°19'S) on 3 Oct. 1995, and died the following day. A Queensland Museum (QM) team arrived at the site on 6 Oct. (Fig. 1). The carcass was flensed and the skeleton collected. The specimen is registered as QMJM11149.

DESCRIPTION

TEETH. Three vestigial maxillary teeth (others were almost certainly present but were lost during flensing) as well as the mandibular teeth were collected (Fig. 2; Table 1). There are 23 right and 23 left mandibular teeth. Beale (1839) counted 24-24 in a specimen from Hull, England. Flower

(1869) examined several specimens in the Museum of the Royal College of Surgeons in London and recorded counts of 20-21 (many teeth were worn and perhaps some were lost), 23-24 and 26-26. Omura et al. (1962) counted 24-24 in a Japanese specimen. One of the first mandibular teeth of QMJM11149 was prepared in section according to Lockyer (1981) and the age estimated at 20 years compared with 32 for the 13.8m male specimen described by Omura et al. (1962).

SKULL. The skull, mandible and hyoid structures [from Omura et al. (1962)] are illustrated in Figs 3 & 4A (measurements, Table 2).

VERTEBRAE. The vertebral formula is C7; D11; L8; Ca25 = 51 compared with C7; D11; L8;



FIG. 1. Sperm whale at Joskeleigh Beach, central Qld coast, 6 Oct., 1995.

Ca24 = 50 for the Tasmanian and Japanese specimens described by Flower (1869) and Omura et al. (1962) respectively. Vertebrae are illustrated laterally in Fig. 5A-E. Fusion of C2-7, characteristic of the species, is demonstrated. A minor developmental anomaly in the spinous process of L6 is evident. It is elongated and its tip has failed to fuse.

The vertebral measurements and the mean vertebral length (MVL) of the Japanese specimen (Omura et al., 1962), are contained in Table 3. $MVL = (a \times b \times c)^{1/3}$ where a, b and c represent the breadth, height and length respectively, of the centra. It was used by Omura (1971) when comparing different baleen whale species. We see no objection to the application of this formula to sperm whales. A comparison between the MVL of QMJM11149 and the Japanese specimen is shown in Fig. 6. (Some difficulty was experienced in co-relating measurements in the cervical vertebrae and, accordingly, those of QMJM11149 have been omitted.)

There are eleven chevrons (Fig. 5F; Table 3). Despite careful dissection, no pelvic bones were recovered, however, a bony structure considered to be a rudimentary femur (Fig. 4B; Table 3) was collected.

RIBS AND STERNUM. There are eleven pairs of ribs (Figs 4C & 7; Table 4). The central foramen in the sternum is noted in the descriptions by Flower (1869) and Omura et al., (1962) and in QMJM9920 (this study). The distal sternal elements in the above specimens show considerable individual developmental variation.

SCAPULAE AND FORELIMBS. Scapulae and forelimb bones are illustrated in Fig. 8 (measurements, Table 5). The phalangeal formula (including the metacarpals) is $I_2, II_{5-6}, III_5, IV_4, V_{3-4}$ compared with $I_1, II_5, III_5, IV_4, V_3$ in the specimen described by Omura et al. (1962).

DISCUSSION

The sperm whale was the most widely hunted cetacean in the 19th and 20th centuries. The question of possible sub-specific status, on the basis of osteological and external features, has interested researchers for more than a century (Flower, 1869). Berzin (1971) noted: 'The only consistent difference found between populations



FIG. 2. Teeth of QMJM11149. Mandibular teeth from right side in upper row and left in lower row. The three vestigial maxillary teeth are shown separately in the lower right. (Scale = 1m)

is that animals from the southern hemisphere have a slightly longer caudal region than those from the northern hemisphere'. Clarke & Paliza (1972) concluded, on the basis of extensive material collected during whaling operations, that sperm whales from the SE Pacific, Japan, the Bonin I. and Durban are not different in their morphometry and accordingly, based on the method of body proportions, did not accept that there are northern and southern sub-species of the sperm whale.

The central epiphyses of the distal caudal vertebrae of QMJM11149 are almost completely fused and presumably further vertebral growth, if the animal had survived, would have occurred predominantly in the dorso-lumbar and proximal caudal vertebrae given the non-fusion of the central epiphyses at those levels (Fig. 5A-D). The MVL of QMJM11149 when compared with the slightly longer male from the Japanese coast (Fig. 6) does not demonstrate a proportional difference in caudal length. On the available osteological data, we are unable to detect any significant difference between the northern and southern hemisphere sperm whale populations.

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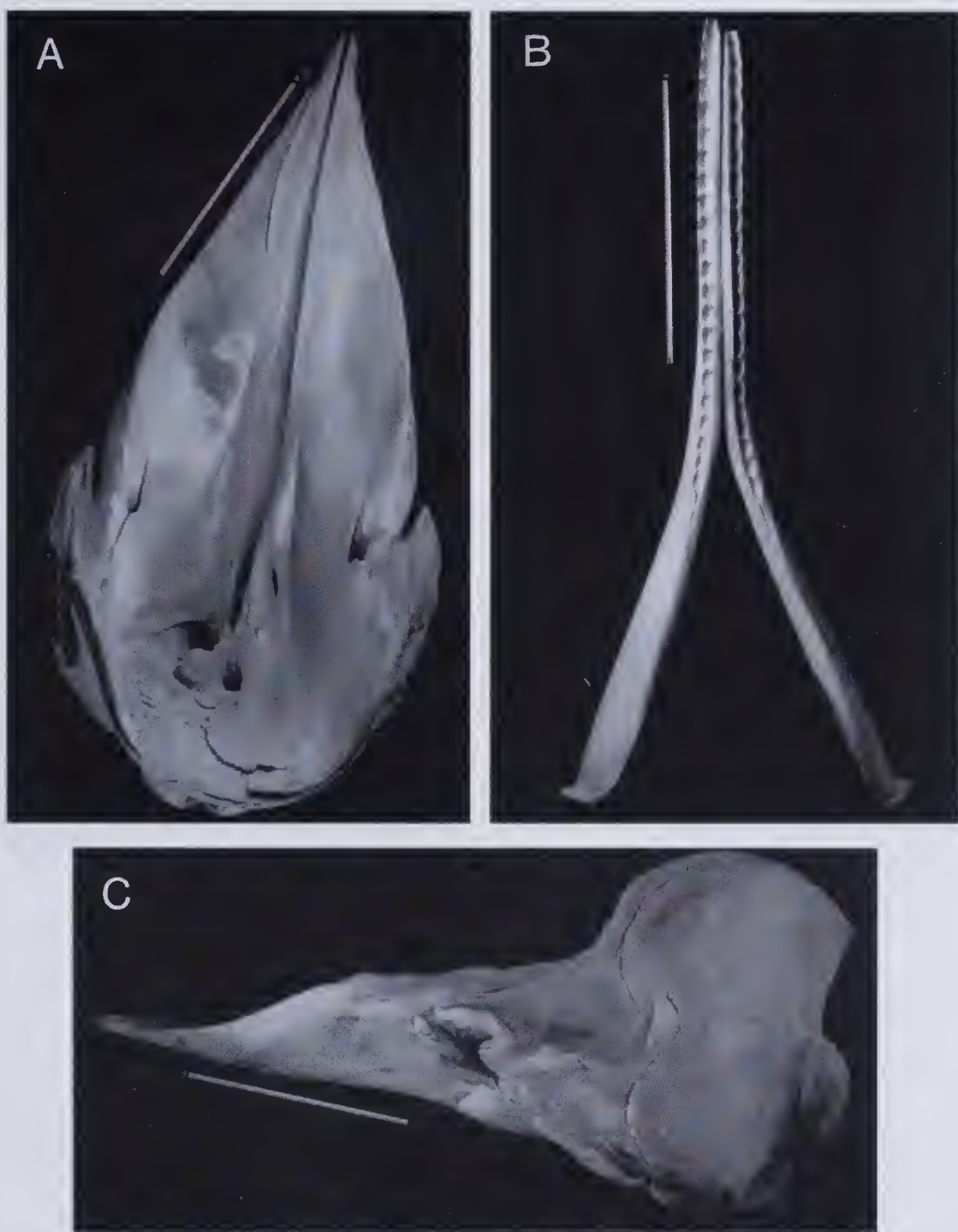


FIG. 3. QMJM11149. A, skull from dorsal aspect; B, mandible from dorsal aspect; C, skull from lateral aspect. (Scales = 1m)

TABLE 1. Mandibular and vestigial maxillary teeth measurements (mm) of QMJM11149. B = broken, * = worn.

Mandibular Teeth	Length		Diameter of cavum dentis (antero-posterior)		Diameter of cavum dentis (transverse)	
	L	R	L	R	L	R
1	88	91*	26	20	17	22
2	88	102*	29	38	20	33
3	101	116	34	42	25	35
4	107	124	37	47	28	35
5	109	125	36	38	36	37
6	109	122	42	52	33	34
7	108	115	44	52	31	36
8	102	115	38	52	35	37
9	116	107	51	34	36	38
10	109	117*	35	53	34	37
11	114	109	50	38	37	38
12	114	112	51	37	36	38
13	116	116	55	38	39	38
14	115	114	53	49	38	35
15	114	95B	55	48	38	37
16	121	114	54	48	47	35
17	115	97B	50	34	38	35
18	114	103*	38	43	36	31
19	114	95*	48	35	35	27
20	124	108	35	38	36	30
21	111*	101	36	38	38	28
22	107	94	42	31	29	29
23	37	80*	20	31	49	18
Maxillary Teeth						
24	58		17		14	
25	46		15		12	
26	50		14		11	

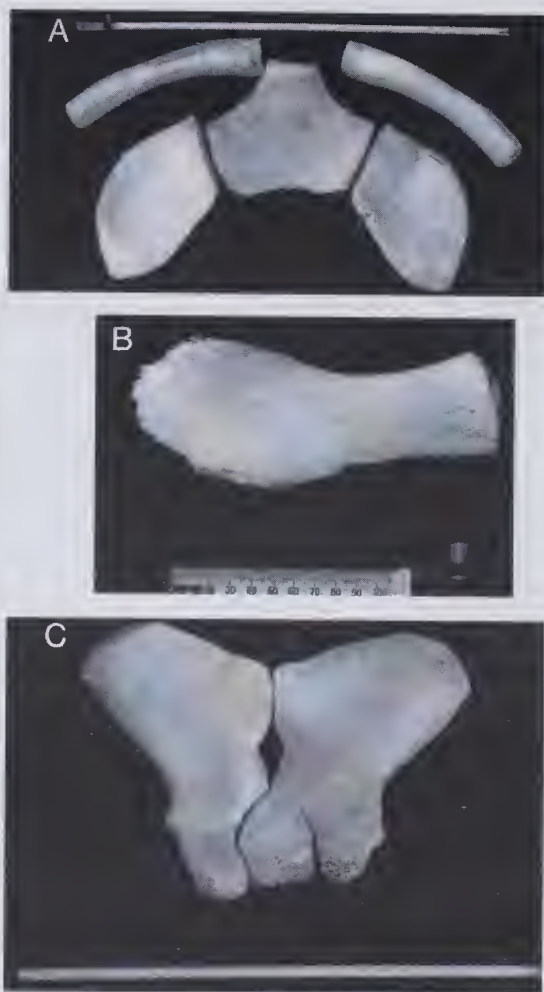


FIG. 4. QMJM11149. A, hyoid components; stylohyals (uppermost), basihyoid (centre), thylohyals (lowermost) (scale = 1m). B, femur (scale in cm). C, sternum (scale = 1m).

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TABLE 2. Skull, mandibular and hyoid measurements (cm) of QMJM11149. * = damaged, # = damaged at tip.

Measurement	cm			
Total (condylo-basal) length	326	Greatest breadth of cranium at parietal region in temporal fossae		
Length of rostrum (median)	249	114		
Breadth of rostrum at base	120	Length of temporal fossae		
Breadth of rostrum at middle	86	L: 32		
Breadth of rostrum between antorbital notches	117	R: *		
Depth of rostrum at middle	18	Depth of temporal fossae		
Breadth of premaxillae at middle of rostrum	23	L: 14		
Breadth of premaxillae in front of anterior nares	53	R: *		
Greatest breadth of premaxillae opposite anterior nares	60	Breadth of occipital condyles		
Least distance between the postero-dorsal margins of the premaxillary foramina	60	49		
Least distance between the postero-dorsal margins of the premaxillary foramina	23	Breadth of foramen magnum		
Least distance between the maxillary foramina and premaxillary foramina	L: 45 R: 32	12		
Greatest breadth of superior nares	27	Length of occipital condyle		
Distance from tip of rostrum to anterior end of vomer	36	L: 32		
Distance from tip of rostrum to anterior margin of superior nares	L: 226 R: 244	R: 34		
Distance from tip of rostrum to medial suture line of posterior end of pterygoid	257	Height, vertex to inferior border of pterygoids		
Distance from tip of rostrum to occipito-frontal vertex	294	109		
Distance from tip of rostrum to posterior median end of maxillary on palate	227	Depth of orbit		
Distance from tip of rostrum to most anterior point of the palatines	227	L: 14		
Length of vomer visible on palate	142	R: 14		
Breadth across middle of orbits	144	Length of mandibular ramus		
Diameter of orbit (antero-posterior)	L: 14 R: 14	L: 269#		
Greatest breadth across supra-orbital plates of maxillae	137	R: 269#		
Greatest breadth across post-orbital processes	147	Distance from anterior end of mandible to coronoid process		
		L: 242#		
		R: 247#		
		Length of symphysis		
		L: 142		
		R: 141		
		Distance from anterior end of mandible to posterior end of alveoli		
		L: 164		
		R: 164		
		Greatest height of mandible at coronoid process		
		L: 43		
		R: 42		
		Distance between mandibular condyles		
		111		
		Distance between ear bones		
		70		
		Breadth of posterior end of pterygoids		
		17		
		Breadth of anterior end of pterygoids		
		49		
		Length of malar bone		
		L: 41		
		R: 41		
		Hyoid	Greatest Length	Greatest Breadth
		Stylohyal, right	47	7
		Stylohyal, left	47	7
		Basihyoid	29	49
		Thylohyal, right	40.5	24
		Thylohyal, left	42	23

TABLE 3. Vertebral, chevron, femoral measurements (mm) and MVL of QMIM11149, MVL of the Japanese specimen. # = unable to calculate.

Vertebra No.	Greatest Breadth	Greatest Height	Centrum Breadth (a)	Centrum Height (b)	Centrum Length (c)	MVL JM11149 ($a \times b \times c$) ^{1/3}	MVL Japanese specimen
C1	683	394	#	#	#	#	127
2-7	637	438	#	#	#	#	243
D1	437	414	237	171	109	164	208
2	436	451	203	109	126	169	199
3	409	471	200	193	127	170	197
4	391	478	190	109	132	170	185
5	384	480	190	181	140	109	186
6	363	479	190	170	145	109	186
7	335	494	197	183	148	175	197
8	323	499	198	185	162	181	198
9	378	508	195	185	170	183	199
10	479	541	202	186	177	188	212
11	520	545	210	203	109	203	221
L1	491	557	200	207	197	203	219
2	480	594	209	207	218	211	233
3	505	589	209	209	245	211	244
4	518	596	210	210	227	218	200
5	531	608	213	220	240	220	254
6	547	615	213	225	230	225	251
7	556	594	214	228	252	231	252
8	567	583	221	232	272	211	260
Cal	561	589	227	233	258	239	273
2	554	508	236	239	279	251	276
3	535	572	242	243	291	258	276
4	490	550	253	245	200	253	279
5	531	525	252	211	282	258	281
6	373	482	250	245	276	257	277
7	320	425	235	237	247	200	265
8	268	384	232	230	233	232	258
9	237	357	215	222	225	221	241

Vertebra No.	Greatest Breadth	Greatest Height	Centrum Breadth (a)	Centrum Height (b)	Centrum Length (c)	MVL JM11149 ($a \times b \times c$) ^{1/3}	MVL Japanese specimen
10	221	325	205	220	212	212	230
11	212	287	198	213	186	190	204
12	203	244	188	200	109	182	173
13	185	200	172	170	118	151	135
14	153	152	142	130	83	115	115
15	151	130	125	112	79	193	104
16	151	125	109	109	74	90	90
17	140	113	85	90	79	81	80
18	121	109	85	80	64	74	76
19	162	85	74	85	55	64	66
20	82	73	65	54	49	56	56
21	85	81	85	37	64	82	53
22	54	56	37	30	10	37	42
23	85	30	33	10	27	30	35
24	29	23	21	10	10	49	24
25	14	13	12	10	10		
Chevron	Greatest Length		Greatest Width				
1	402		100				
2	100		187				
3	393		195				
4	374		182				
5	340		195				
6	280		185				
7	242		100				
8	100		100				
9	100		150				
10	123		100				
11	100		10				
Femur	179		10				

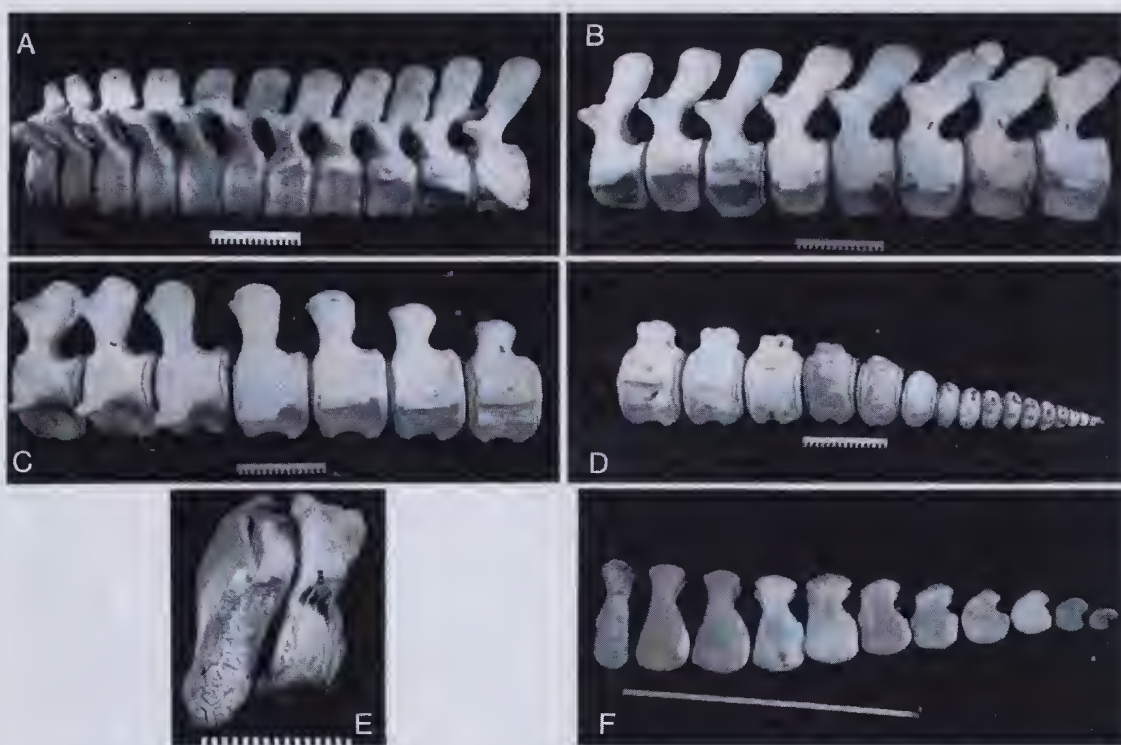


FIG. 5. Vertebrae of QMJM11149 from lateral aspect; A, dorsal; B, lumbar; C & D, caudal; E, cervical; (scales in cm). F, chevrons (scale = 1m).

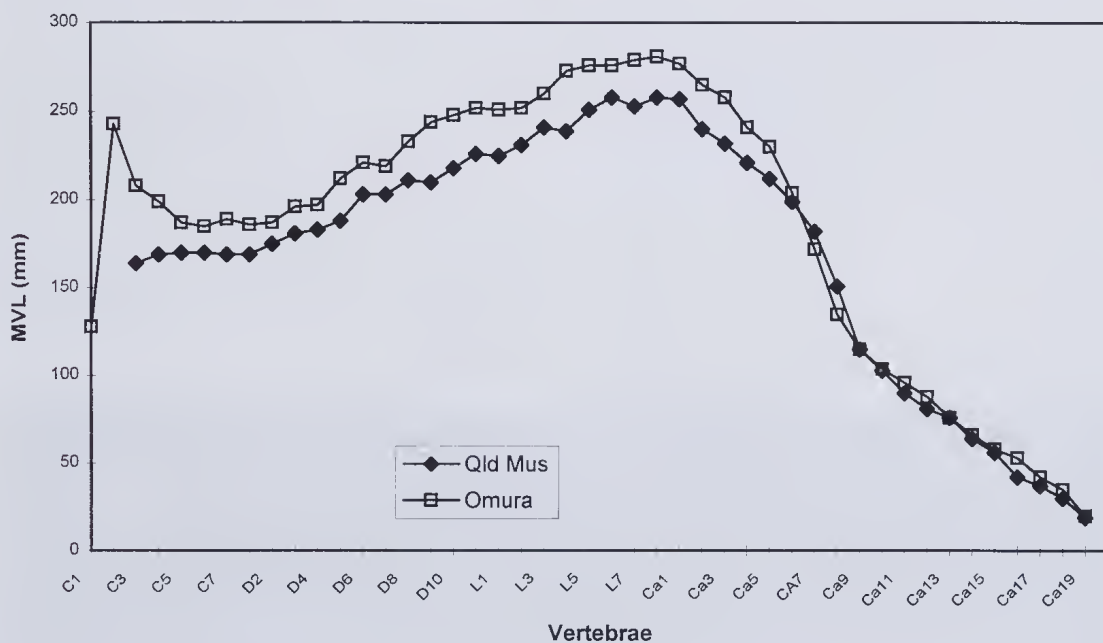


FIG. 6. Comparison between mean vertebral lengths (MVL) of QMJM11149 and the Japanese specimen (Omura et al., 1962).

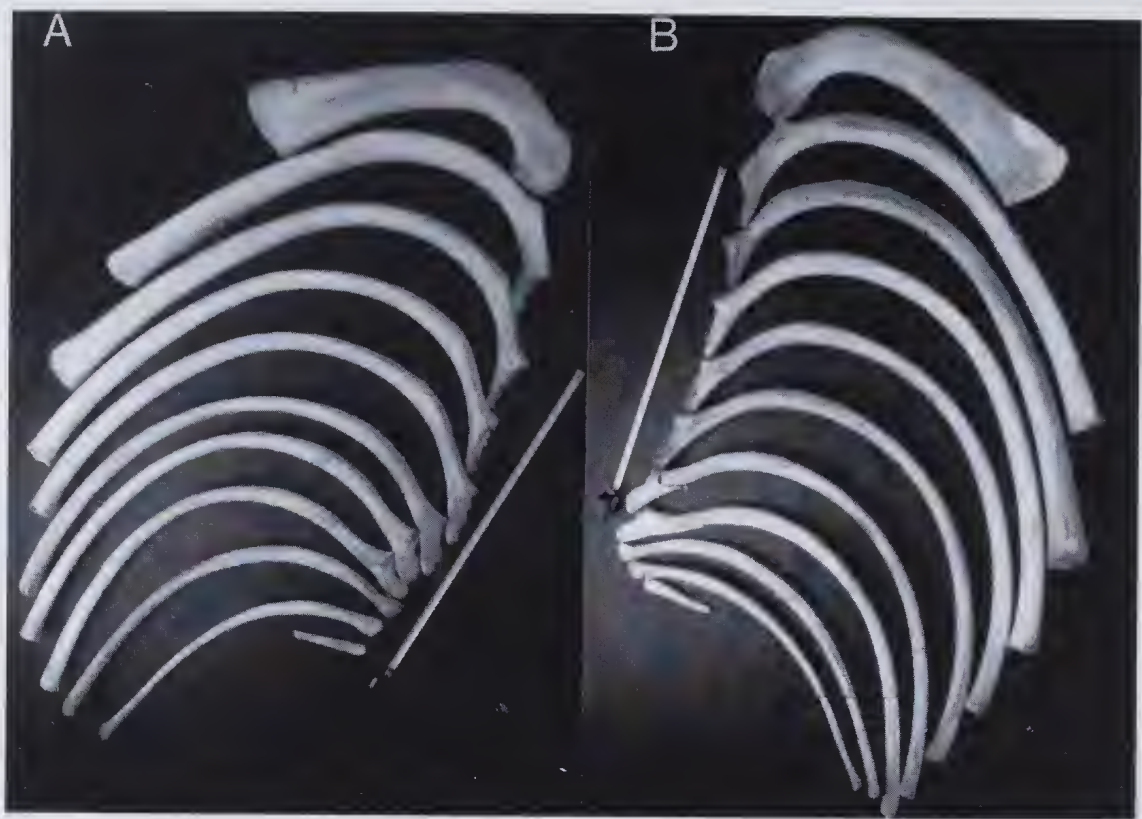


FIG. 7. Ribs of QMJM11149; A, left; B, right. (Scale = 1m)

TABLE 4. Rib and sternal measurements (cm) of QMJM11149. * = damaged.

Rib	Straight Length		Rib	Straight Length	
	Left	Right		Left	Right
1	93	94	9	123	114*
2	129	128	9	112	110
3	142	141	10	95	94
4	142	139	11	22	23
5	135	133	Sternum	Greatest Length	Greatest Width
6	135	130	Left side	58	42
7	128	126*	Right side	54	42

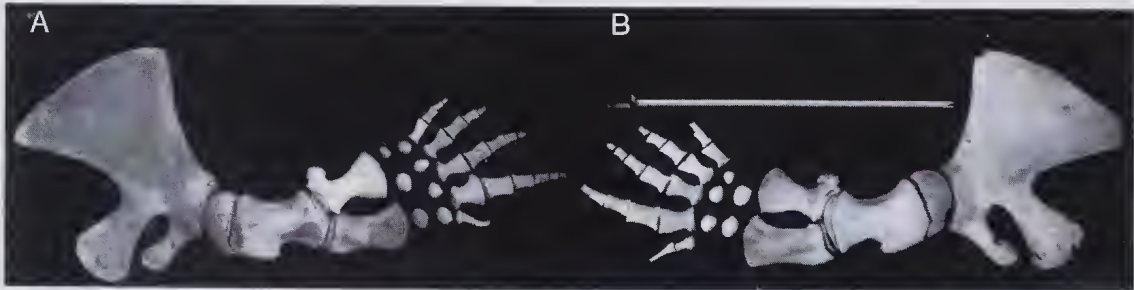


FIG. 8. Scapulae and forelimb bones of QMJM11149; A, left; B, right; (scale = 1m).

TABLE 5. Scapular and forelimb measurements (mm) of QMJM11149. * = possibly missing.

Scapula					Humerus, Radius, Ulna							
							Width at centre		Length			
Greatest Breadth					545	550	Left		Right	Left	Right	
Greatest Length					615	605	Humerus		130	130	370	367
							Radius		114	93	258	256
							Ulna		81	88	244	234
Length of Phalanges												
Phalanx	Left					Right						
	I	II	III	IV	V	V	II	III	IV	I		
I	63	99	99	99	99	61	101	103	63	73		
2	51	88	74	65	52	88	93	99	69	53		
3		67	57	48	30		76	62	51	33		
4		45	38	31	18		49	39	33	*		
5		30	24				33	27				
6		14										

IRRAWADDY DOLPHINS *ORCAELLA BREVIROSTRIS* (OWEN IN GRAY) FROM SOUTHERN QUEENSLAND. *Memoirs of the Queensland Museum* 42(2): 554. 1998:- The Irrawaddy dolphin is an inshore species regularly recorded from north Queensland. Most Queensland Museum records derive from shark nets (Paterson, 1994). The previous southernmost record is QMJM10574 from Bundaberg (24° 52'S, 152° 21'E). We report sightings, presumably of Irrawaddy dolphins, from the Brisbane and Bremer Rivers in June/July 1997 and a confirmed record for the species based on the collection of a carcass on 23 July, 1997 from the Brisbane R. at Karana Downs (27° 32'S, 152° 49'E).

Dolphins were sighted on three separate occasions from ~ 11-22 June at the Moggill Ferry in the turbid upper tidal reaches of the Brisbane R. (72km from the mouth). A pair was seen initially and the two subsequent sightings were of single animals. On 24 June a single animal was seen from 10am-noon near Kookaburra Park, Karana Downs (82.5km from the mouth). It passed the observation point 5-6 times and appeared to be chasing mullet in the relatively clear water. It was lighter grey than a bottlenose dolphin (*Tursiops truncatus*) and to one observer it was 'ghostly coloured', and to another 'looked like it might have been sick'. It was approached by canoe and noted as 'very pale ... even pink or greyish pink ... with a big forehead'. Photography (Fig. 1) confirmed a blow and a blunt, rounded forehead with no obvious beak. A dolphin, presumably the same animal, was seen the next day at that location. On 17 July a further sighting was reported from the Bremer R., the major tributary of the Brisbane R., 3.4km from the junction, a point 1.3km upstream from the Moggill Ferry. The observers, the crew of the coal barge C.R. Campbell, did not note specific characteristics. Contact was maintained for 20 min. as the animal moved downstream. The crew considered the sighting unusual, as dolphins are rarely encountered upstream from the Gateway Bridge (10km from the mouth of the Brisbane R.).

On 20 July a dolphin carcass was found floating in the Karana Downs section of the Brisbane R. ~ 85km from the mouth. This is ~ 4km below the limit of tidal influence (Steele, 1990). The decomposed 1.98m long specimen was collected by RAP and SVD. Sex and cause of death could not be determined. The skull (Fig. 2) and skeleton registered as QMJM11976, clearly establish the dolphin as an adult *Orcaella brevirostris* [for diagnostic characters see Arnold & Heinsohn (1996)].

All observations and the collection of QMJM11976 occurred in essentially freshwater (Davie, 1990). This and the descriptions on 24 June are typical of *O. brevirostris* (Cawardine, 1995).



FIG. 1. Presumed *Orcaella brevirostris* at Karana Downs, Brisbane River 24 June, 1997.

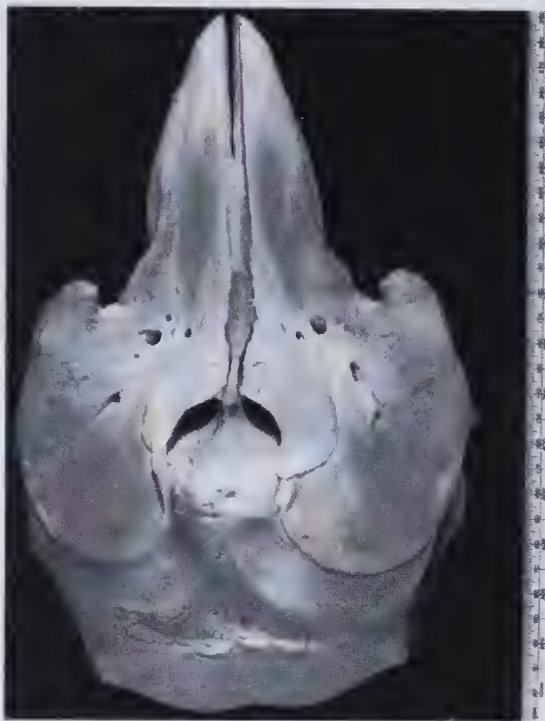


FIG. 2. Skull (dorsal aspect) of QMJM11976.

Public interest created reflects the unusual occurrence of dolphins in the upper tidal reaches of the Brisbane R. Accordingly, although this record extends the distribution of *O. brevirostris*, it is likely that the dolphins were vagrants.

Acknowledgements

Bruce Gynther discovered and secured the specimen. Roy Ashwell, Jacob Clarke, Daniel Humphreys, Ian Lewis, Alan Macarthur and Tom Watkins provided sighting information. Tom Watkins gave us the photographs taken by Jacob Clarke. Brother McGee of St Edmund's College and Barry Sampson Searle assisted in contacting observers. Heather Janetzki prepared the specimen and Jeff Wright photographed the skull.

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PREDATION ON DIURNAL INSECTS BY THE EASTERN HORSESHOE BAT,
RHINOLOPHUS MEGAPHYLLUS GRAY (CHIROPTERA: RHINOLOPHIDAE)

CHRISTOPH R. PAVEY AND CHRISTOPHER J. BURWELL

Pavey, C.R. & Burwell, C.J. 1998 06 29: Predation on diurnal insects by the Eastern Horseshoe Bat, *Rhinolophus megaphyllus* (Chiroptera: Rhinolophidae). *Memoirs of the Queensland Museum* 42(2): 555-558. Brisbane. ISSN 0079-8835.

Insectivorous bats exhibit crepuscular activity despite being very vulnerable to predation by diurnal birds at such times. For this behaviour to persist the benefit(s) of crepuscular activity must balance or outweigh the costs. This study established that the Eastern Horseshoe Bat, *Rhinolophus megaphyllus*, captured diurnal insects from three orders; butterflies (Lepidoptera), dragonflies (Odonata) and cicadas (Hemiptera), during crepuscular activity. Diurnal prey were eaten at four roosts in eastern Queensland where prey remains were regularly collected and at three roosts where remains were collected opportunistically. The amount of predation on diurnal insects varied between the four roosts, and overall it was low. The emergence time of *R. megaphyllus* also varied between roosts with bats emerging earlier in rainforest than woodland. Earlier emergence occurred at the roost where predation on diurnal insects was most frequent. This study indicates that a possible benefit of crepuscular activity to *R. megaphyllus* is the availability of diurnal insects as prey. □ *Rhinolophus megaphyllus*, predation, diurnal insects, crepuscular activity.

Chris R. Pavey, 64 Arafura Street, Upper Mt Gravatt, Queensland 4122, Australia; Chris J. Burwell, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 1 November 1997.

Many species of insectivorous bats have crepuscular activity, whereby they depart from their roosts during the period of civil twilight after sunset but prior to dark (Jones & Rydell, 1994). Insectivorous bats appear to be very vulnerable to predation by diurnal and crepuscular birds at such times (Young, 1980; Neuweiler et al., 1987; Speakman, 1991, 1995; Fenton et al., 1994; Jones et al., 1995). Bats are available as prey to diurnal and crepuscular birds only during the short time period at dusk and dawn when the activity rhythms of predator and prey overlap. Because diurnal and crepuscular birds can hunt only in daylight, twilight or moonlight, insectivorous bats could avoid predation by emerging after dark (Erkert, 1978; Black et al., 1979; Fenton, 1995). However, the evolution of a predator such as the Bat Hawk, *Macheiramphus alcinus* Bonaparte, with specialised adaptations for the capture of bats at dusk (Fenton et al., 1977; Black et al., 1979; Fenton, 1995), clearly demonstrates that crepuscular activity has persisted over evolutionary time.

The costs associated with crepuscular activity must be balanced or outweighed by benefits for the behaviour to persist. One potential benefit is that bats have access to diurnal insects, a term here used to include both diurnal and crepuscular species, during the dusk period (Black et al., 1979; Fenton et al., 1994). If this interpretation is

correct, bats that show crepuscular activity should regularly capture diurnal insects. The current study sought to examine this possibility by determining the amount of predation on diurnal insects by the Eastern Horseshoe Bat, *Rhinolophus megaphyllus* Gray, 1834, a species of insectivorous bat known to be active at dusk.

METHODS

STUDY SPECIES. *Rhinolophus megaphyllus* is a relatively small bat (7-14g) which occurs in eastern Australia from Cape York Peninsula to central Victoria. This species captures insects using CF-FM (constant frequency-frequency modulated) echolocation calls emitted at high duty cycles (Jones & Corben, 1993; de Oliveira & Schulz, 1997). A large amount of experimental and observational evidence indicates that the echolocation calls of members of the genus *Rhinolophus* restrict them to the capture of insects that are either flying or sitting with fluttering wings (Link et al., 1986; Neuweiler et al., 1987; Rübsamen et al., 1988; Neuweiler, 1989, 1990; Emde & Schnitzler, 1990). This restriction is also likely to apply to *R. megaphyllus* (Pavey, 1995), so it cannot capture diurnal insects resting on foliage at night. Therefore, any diurnal insects in the diet are almost certainly captured when the insects are active.

FIELD SITES. The study was conducted at roosts of *R. megaphyllus* located in disused mines in eastern Queensland. Dietary data were collected from four roosts which, from S to N, were at Anduramba (27°09'S, 152°07'E), Conondale Ra. (26°39'S, 152°39'E), Irvinebank (17°26'S, 145°12'E) and Atherton (17°20'S, 145°26'E). Collections were made on 17, 19, 3 and 8 visits, respectively, to each roost. In addition, diurnal insects were found among prey remains in roosts at Mt Molloy (16°43'S, 145°20'E), Herberton (17°24'S, 145°24'E), Paluma (19°01'S, 146°13'E) and Iron Ra. (12°43'S, 143°18'E). Collections were made during a single visit to each of these roosts. The Conondale Ra., Paluma and Iron Ra. roosts were located within rainforest, whereas other roosts were located in eucalypt open forest or woodland. All sites were located away from sources of artificial light that may have attracted diurnal insects. None of the species of diurnal insects recorded as prey of *R. megaphyllus* in this study were observed in any of the roosts.

DIETARY DATA. The incidence of diurnal insects in the diet was determined by identifying remains of prey discarded by bats which had returned to diurnal roosts to feed. Prey remains, mostly wings, were collected by thoroughly searching the floor of each roost using a head torch. Remains were identified by comparison with pinned specimens at the University of Queensland Insect Collection and Queensland Museum. Most wings could be identified to family, and most lepidopteran material to species or genus. The minimum number of individuals of each prey taxon in each collection (site and date specific) was calculated by using the forewing or hindwing with the highest count.

Entomological literature was the source for verifying the activity rhythms of prey taxa that were potentially diurnal. The following texts were the primary references employed; Common, 1990 (Lepidoptera, excluding superfamily Papilionoidea); Common & Waterhouse, 1981 (superfamily Papilionoidea – butterflies); Watson et al., 1991 (Odonata); Moulds, 1990 (Cicadidae); CSIRO Division of Entomology, 1991 (other orders). If no information was available on the activity rhythms of a particular species or genus, it was assigned the activity pattern that was most characteristic of its family.

EMERGENCE TIME OF BATS. The time of departure was recorded for the colonies of *R. megaphyllus* at Anduramba (7 nights) and Conondale Ra. (3 nights), but not at Irvinebank

TABLE 1. List of diurnal families and species of insects captured by *Rhinolophus megaphyllus* (n=35 prey items). A damselfly (Order Odonata, Suborder Zygoptera) from Conondale Ra. that could not be identified to family is not included.

Order/Family	Species	Sites (No. Taken)
Lepidoptera		
Hesperiidae	<i>Hasora khoda</i>	Conondale Ra. (1)
	<i>Euschemon rafflesia</i>	Paluma (1)
	<i>Chaetocneme beata</i>	Conondale Ra. (9)
Pieridae	<i>Eurema</i> sp.	Mt Molloy (1)
Nymphalidae	<i>Melanitis leda</i>	Conondale Ra. (1) Mt Molloy (1)
	<i>Hypocysta adiante</i>	Atherton (1)
Lycaenidae	<i>Hypochrysops miskini</i>	Atherton (1)
Odonata		
Aeshnidae	<i>Antipodophlebia asthenes</i>	Conondale Ra. (2)
	<i>Austrogynacantha</i> or <i>Gynacantha</i> sp.	Iron Range (1)
	unidentified spp.	Conondale Ra. (4) Mt Molloy (1) Iron Ra. (1)
Libellulidae	<i>Agrionoptera</i> sp.	Iron Ra. (1)
	<i>Tholymis tillarga</i>	Iron Ra. (1)
	<i>Orthetrum</i> sp.	Anduramba (1)
Hemiptera		
Cicadidae	unidentified spp.	Conondale Ra. (2) Atherton (2) Irvinebank (2)

or Atherton. Observations were conducted on nights with no rain or strong wind and during all phases of the moon. An observer, positioned within 20m of the entrance of each roost, counted the bats as they emerged in the evening. The time of first emergence was recorded, and also the time of darkness (when he was no longer able to see well enough to walk without the aid of artificial light).

RESULTS

DIET. A total of 830 insects was recorded among prey remains of *R. megaphyllus* at the four roosts. The number of prey items and number of diurnal insects recorded at each site were: Anduramba, 118 prey items (1 diurnal insect); Conondale Ra., 471 (20); Irvinebank, 53 (2); and Atherton, 188 (4). Diurnal insects made up 3.25% (n=27) of the combined total of insect prey. The percentage of diurnal insects among prey items varied across sites, ranging between 0.85% at Anduramba and 4.25% at Conondale Ra. In addition, eight diurnal insects were recorded among prey remains at Mt Molloy (3), Paluma (1) and Iron Ra. (4) (Table 1).

Diurnal insects taken were predominantly Lepidoptera (16) and Odonata (13), although a smaller number of Hemiptera, all cicadas (6), were captured (Table 1). All individuals taken were winged adults. In total, seven families of diurnal insects were taken by *R. megaphyllus* during the study. The HesperIIDae (skippers) was the most frequently taken family. Other insect orders were recorded among prey remains, but they did not include species that were definitely known to be diurnal.

POTENTIAL PREDATORS. A number of species of diurnal birds known to feed on bats (Young, 1980; Marchant & Higgins, 1993; Speakman et al., 1994) were sighted during incidental observations at the study sites. These species were: Collared Sparrowhawk *Accipiter cirrhocephalus* (Vieillot), Peregrine Falcon *Falco peregrinus* Tunstall, Australian Hobby *F. longipennis* Swainson, Nankeen Kestrel *F. cenchroides* Vigors & Horsfield, Laughing Kookaburra *Dacelo novaeguineae* (Hermann), Pied Butcherbird *Cracticus nigrogularis* (Gould), Grey Butcherbird *C. torquatus* (Latham) and Pied Currawong *Strepera graculina* (Shaw). Two of these species, Grey Butcherbird and Pied Currawong, were sometimes attracted to the entrances of roosts when bats were released during daylight.

EMERGENCE TIME OF BATS. The mean emergence time of the colony at Anduramba, which was located in woodland, was 29 minutes after sunset (1.62 SE). This emergence time was, on average, 9 minutes (3.34 SE) prior to darkness. Colony size during the counts ranged from 21 to 91 individuals. The mean emergence time of the colony at Conondale Ra., which was located in rainforest, was 4 minutes prior to sunset (2.08 SE). This emergence time was, on average, 39 minutes (3.79 SE) prior to darkness. Colony size during the counts ranged from 100 to 380 bats.

DISCUSSION

This study investigated the hypothesis that bats exhibit crepuscular activity as a means of gaining access to diurnal insects. *Rhinolophus megaphyllus*, a species that is active at dusk, did feed on diurnal insects. Current knowledge of the foraging ecology and auditory capacities of this species, and other members of its genus, indicates that diurnal insects were captured while they were active rather than while resting on vegetation at night. Also, none of the species of diurnal insects captured (Table 1) was observed roosting in dis-

used mines. Therefore, bats probably did not capture diurnal insects in roosts.

The frequency of predation on diurnal insects pooled across the four roosts was one in every 30 prey items (3.25%). This frequency is low, although not unexpected given the short duration of dusk within the study area. In SE Queensland the time between sunset and the following sunrise ranges from a maximum of about 800 minutes in June to a minimum of 600 minutes in December. The duration of dusk, the time between sunset and dark, is only 30 to 45 minutes. Therefore, dusk represents between 4 and 8% of potential foraging time. The rate of predation on diurnal insects was thus lower than the proportion of available foraging time taken up by the dusk period.

Overall, the study provides preliminary support for the hypothesis that bats forage at dusk in order to gain access to diurnal insects. However, other explanations are possible. Bats may depart their roosts at dusk in order to commute to distant foraging areas which are only reached after dark. Alternatively, bats may forage on early flying nocturnal species during dusk, with diurnal species being captured incidentally. Clearly, more research is needed before definitive conclusions can be drawn.

The amount of predation on diurnal insects by *R. megaphyllus* varied between colonies. The lowest predation rate was in woodland at Anduramba (0.85%). The highest rate was in rainforest at Conondale Ra. (4.25%). The departure times of bats also differed between the two roosts. Bats at Anduramba began emerging 29 minutes after sunset, whereas those at Conondale Ra. began emerging 4 minutes prior to sunset. The difference in departure times was probably caused by the dense canopy of rainforest at Conondale Ra., which restricted the penetration of light at the mine entrance in the late afternoon. Thus bats emerged when light levels were low in rainforest adjacent to the roost, but still quite high in nearby open forest in which they foraged (C. Pavey, unpub. obs.). Earlier emergence at roosts with greater cover has been observed for other species of bats (e.g., Jones et al., 1995).

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A NEW SPECIES OF *DERO* (*ALLODERO*) (NAIDIDAE: OLIGOCHAETA)
INHABITING THE WOLFFIAN DUCTS OF THE GREEN TREE FROG
(*LITORIA CAERULEA*) IN QUEENSLAND

ADRIAN M. PINDER, BRUCE D. HILL AND PETER E. GREEN

Pinder, A.M., Hill, B.D. & Green, P.E. 1998 06 29: A new species of *Dero* (*Allodero*) (Naididae: Oligochaeta) inhabiting the Wolffian Ducts of the Green Tree Frog (*Litoria caerulea*) in Queensland. *Memoirs of the Queensland Museum* 42(2): 559-564. Brisbane. ISSN 0079-8835.

A new species of naidid oligochaete, *Dero* (*Allodero*) *litoria*, inhabiting the ureters of the Green Tree Frog (*Litoria caerulea*), is described from Queensland. This is the first record of this subgenus from Australia. The new species is most similar to *Allodero hylae* (Goodchild, 1951) of SE USA, from which it is distinguished by having gills within a branchial fossa and mid-segmental dorsal ridges which extend around to the ventral setae. □ *Oligochaeta*, *Naididae*, *new species*, *amphibia*, *commensalism*, *Queensland*, *Australia*.

Adrian M. Pinder, Western Australia Museum, Francis Street, Perth 6001, Western Australia (present address, Wildlife Research Centre, Department of Conservation and Land Management, P.O. Box 51, Wanneroo 6065, Western Australia); Bruce D. Hill, Department of Primary Industries, Rockhampton Veterinary Laboratory, Box 6014, Rockhampton Mail Centre 4702, Queensland; Peter E. Green, Department of Primary Industries, Animal Research Institute, Locked Mail Bag No. 4, Moorooka 4105, Queensland, Australia; 28 July, 1997.

Dero Oken, 1815 (Naididae) is diagnosed by a fossa (cavity) around the anus, which usually contains gill filaments. Three subgenera, *Aulophorus*, *Dero* and *Allodero* are usually recognised. The first two are very similar: both have ventral setae that are longer and thinner on anterior segments than on posterior segments, a full complement of dorsal setae, a well developed branchial fossa and gills and all species are free-living. They differ from each other only in that *Dero* lacks the pair of elongate palps found on the posterior border of the *Aulophorus* fossa. By contrast, *Allodero* is mostly endocommensal in frogs, have all ventral setae similar and (especially in commensal specimens) the dorsal setae and branchial organs are often reduced or absent.

There are seven species in *Allodero*. Five of these, *A. bauch-iensis* (Stephenson, 1930), *A. hylae* (Goodchild, 1951), *A. lutzi* (Michaelsen, 1926a), *A. floridana* Harman, 1971, and the new species, are known to be endocommensal in frogs, although at least one (*A. lutzi*) can exist in a free-living state. A sixth, *A. malayana* (Stephenson, 1931) has so far only been found free-living.

The new species described in this paper is the first record of the subgenus in Australia, although the other two subgenera have been recorded previously (Brinkhurst 1971; Pinder & Brinkhurst, 1994). It is only the second species of Naididae to be recorded only from Australia, the other being a species of *Slavina* Pinder & Brinkhurst, 1998).

The other 29 species recorded in Australia (Pinder & Brinkhurst, 1994) also occur in other continents.

Discovery of the new species of *Allodero* was an incidental finding made during dissection of Green Tree Frogs (*Litoria caerulea*). The frogs had been submitted to the Rockhampton Veterinary Laboratory by a farmer who wished to know why so many of this species were found in poor condition in her locality. All worm specimens have been deposited with the Queensland Museum (QM).

Very few oligochaetes have taken to a symbiotic lifestyle compared to the other major clitellate group, the leeches. Gelder (1980) reviewed symbiotic relationships between 13 species of Enchytraeidae, Naididae and Haplotaenidae and their hosts (worms, molluscs, crustaceans and fish). In addition, three Phreodrilidae of the genus *Astacopsidrilus* have been found to be ectocommensal on *Euastacus* crayfish in Australia (Goddard, 1909; Brinkhurst, 1991; Pinder & Brinkhurst, 1997). Most relationships appear to involve ectocommensalism, with endocommensalism and endoparasitism restricted to *Allodero* and another naidid *Chaetogaster limnaei* von Baer, 1827 (Gelder, 1980). The cosmopolitan *C. limnaei* is endo- or ectocommensal, or even parasitic (depending on the subspecies) on molluscs. In Australia, it has been found to inhabit the pulmonary chamber and body surface of several lymnaeid and planorbid gastropods (Davies, 1913).

MATERIALS AND METHODS

Between Feb., 1996 and Jan., 1997 the farmer submitted a total of 52 Green Tree Frogs (27 ♂♂ and 25 ♀♀) to the laboratory to establish a reason for their apparent ill health. The number of frogs collected and the frequency of the submissions was determined only by the time available to the farmer. Soon after collection they were brought to the laboratory, sacrificed by pithing and then dissected to remove various internal organs for examination. The kidneys and Wolffian ducts were dissected free and placed in a petri dish containing phosphate buffered saline (pH 7.1). Using a dissecting microscope, fine scissors and forceps the Wolffian ducts were opened along their length. Oligochaetes were removed and placed in 70% alcohol. Tissues intended for histological examination were fixed in 10% buffered neutral formalin, embedded in paraffin and stained with haematoxylin and eosin using routine methods.

Alcohol preserved specimens were either mounted in CMCP-10 or stained in Grenacher's Borax Carmine, then cleared in methyl salicylate and mounted in Permount.

The following abbreviations are used in the figures. *Allodero lutzi*: b=brain, bf=branchial fossa, bu=buccal canal, c=coelomocytes, cu=cuticle, cg=chlorogogen tissue, e=epidermis/epidermal cell, g=gill, i=intestine, m=mouth, mu=body wall muscle, n=nerve cord, p=pharynx, pg=pharyngeal gland tissue, rm=retractor muscles. *Litoria caerulea*: le=luminal epithelium of wolffian duct, kp=kidney parenchyma.

SYSTEMATICS

Phylum ANNELIDA
Class OLIGOCHAETA
Family NAIDIDAE

Dero Oken, 1815

Dero (Allodero) litoria sp. nov.
(Figs 1-4)

MATERIAL. HOLOTYPE: QMG213863. Immature on slide, found on Green Tree Frog (*Litoria caerulea*) collected on farmland, Mt Larcom, 23.87°S 150.91°E, central Queensland, between ii.1996 and i.1997, coll. H.A. Luckey. PARATYPES: QMG213864 - 213869, 213871 - 213874 and 213877 (11 slide mounted immatures); 16 alcohol specimens (in three vials), QMG213870, 213875 and 213876. Collection details as for holotype.

DESCRIPTION. Dimensions (preserved and slide mounted) 3.2mm × 170µm (49 segments) to 6.2mm × 350µm (79 segments). Colour reddish-brown when alive. Anal end of some specimens

without setae and not clearly segmented while anal ends of other specimens terminating abruptly and obviously incomplete, but with intact (or almost intact) body wall, indicating recent regeneration and possibly asexual reproduction by fragmentation. Budding not evident. A ring of thickened body wall occurring towards the posterior of each segment (Fig. 1C), creating a ring level with the setae. This is most noticeable dorsally (Fig. 1A) and at the ventral setal bundles, so that the dorsal setae occur on a ridge and the ventral setae appear to protrude from papillae, and is least developed ventrally. This ring is created by enlargement and bunching up of the epidermal cells (Fig. 1C).

Alimentary canal difficult to make out and possibly not continuous in some specimens. Generally, a thin walled buccal canal (Fig. 1A) leads from mouth to a thickened pharynx in III and IV, with muscular attachments to dorsal body wall of III. Pharyngeal gland tissue present in III to IV or V (Fig. 1A). Lumen in gut very narrow (Fig. 1A) or not visible. No gut contents visible. In one specimen, which has a prostomium and brain, so is otherwise developed anteriorly, there appears to be no mouth, buccal cavity and pharynx. Posterior gut often difficult to trace but (in fully regenerated specimens) dorsal anus present on the last segment. Gut and dorsal blood vessel surrounded by masses of brown chlorogogen tissue from VI onwards (Figs 1A, 3), which often fills the entire coelomic cavity of some segments. Chlorogogen cells elongate tear-drop shaped, arising from the wall of the intestine, with a large deeply staining nucleus and coarsely granular cytoplasm. Sub-spherical coelomocytes present, with cytoplasm more transparent than that of the chlorogogen cells. Coelomocytes (Fig. 1A) either free or lying adjacent to the chlorogogen or body wall, varying in density from sparse to filling the coelom between the body wall and chlorogogen. Some specimens with a branchial fossa, varying in development from barely apparent to an obvious chamber. In two specimens the fossa contains two pairs of short, rounded, knob-like gill filaments, not protruding from the fossa (Fig. 1B). The gut and branchial fossa appear to be most developed when the dorsal setae are also most numerous.

Bifid ventral setae from II (Fig. 2A-C), 4 to 6 per bundle anteriorly, usually 3 or 4, rarely 2 or 5 per bundle posteriorly, most 72.5-92.5µm long with a slightly distal nodulus. Setae of II-VI (Fig. 2A,B) not especially longer and thinner than those in following segments (Fig. 2C), although the most posterior setae often slightly shorter

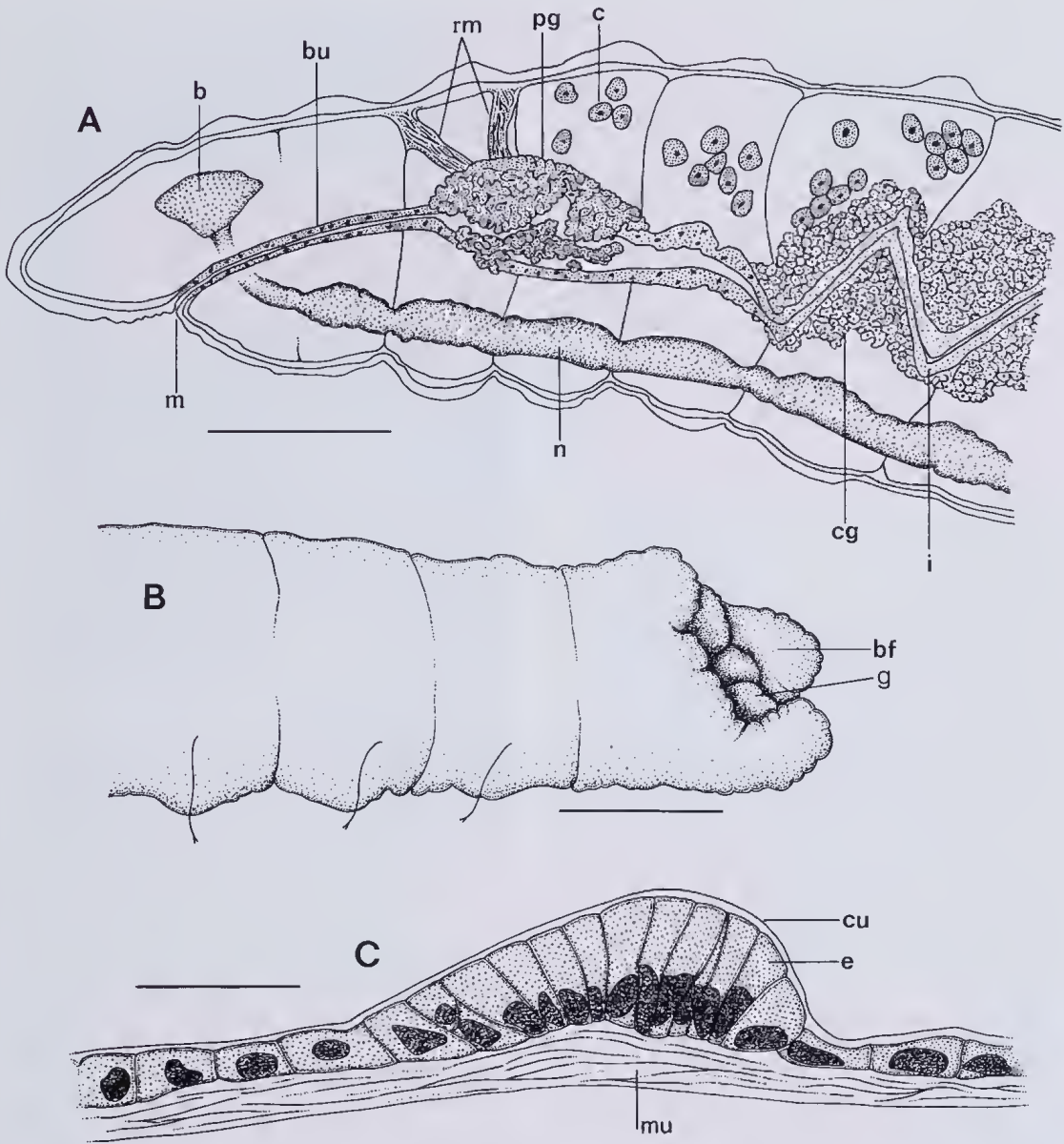


FIG. 1. *Allodero litoria* sp. nov. A, anterior seven segments, based on paratype G213865 with details from other specimens; B, posterior end of holotype showing three of the four gills, the fourth is obscured by the dorsal wall of the fossa; C, section of dorsal body wall of paratype G213867 showing ridge created by enlarged and bunched epithelial cells. Scales: A=100 μ m, B=80 μ m, C=20 μ m.

(62.5–70 μ m) and the nodulus slightly more distal anteriorly. Dorsal setae from IV, often absent in some segments or absent entirely in some specimens. Each bundle with 1 or 2 needles (55–73 μ m long) with a distal nodulus, bifid tips with short curved outer teeth, the lower tooth much thicker and somewhat longer than the upper, often with a third very

small intermediate tooth (Fig. 2D, E). One short hair (95 μ m long) present in one bundle of a single specimen, accompanied by 2 needles (Fig. 2F).

Worms found within the ureters of *Litoria caerulea* (Figs 3, 4).

DISTRIBUTION. *Allodero* is circum-tropical (Africa, SE Asia, Central and South America and

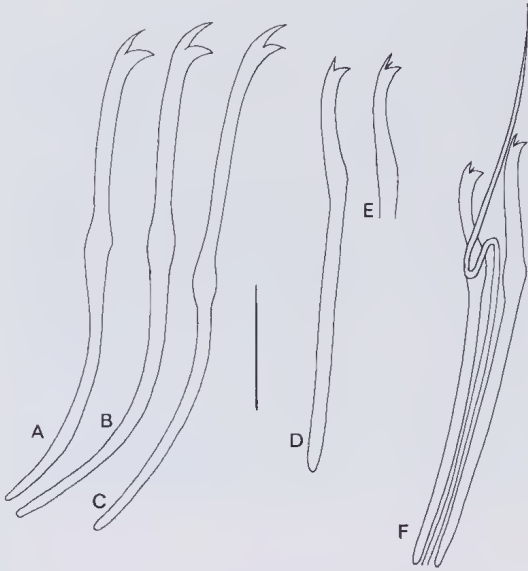


FIG. 2. *Allodero litoria* sp. nov. A, ventral seta of III; B, ventral seta of V; C, ventral seta of a posterior segment; D, dorsal needle with bifid tip; E, tip of dorsal needle with intermediate tooth; F, hair and needle setae of XVI of paratype G213864. Scale = 20µm.

SE North America). The new species from Mt Larcom (23.87°S 150.91°E) fits this pattern. Full distribution of the species in Australia has not been determined. The frog host species is widely distributed in N and E Australia. Host frogs were found several hundred metres from the nearest water (farm dams).

ETYMOLOGY. For the frog host.

REMARKS. The presence of a gilled branchial fossa places the new species in *Dero*, while the endocommensal habit, uniform ventral setae and a tendency to lose the dorsal setae and fossa indicates its placement in the subgenus *Allodero*.

The new species is most similar to *A. hylae*, which inhabits the ureters of various species of *Hyla* (Hylidae) in SE USA (Harman & Lawler, 1975). The setae of *A. hylae* are of similar size and form to those of *A. litoria*, except that the needles of the former are usually one per bundle (one or two in *A. litoria*) and do not have intermediate teeth. Intermediate teeth are otherwise known only from *A. floridiana* but in that species they are much more pronounced (Harman, 1971). However, the presence or absence of intermediate teeth on bifid setae is considered a poor character for species separation in *Dero* and other naidids (Grimm, 1987). *A. hylae* also has papillae at the position of the dorsal setae and the illustrations of

Goodchild (1951) show these to be similar to the ridges of *A. litoria*, except that those of *A. hylae* do not extend to the ventral setae according to Goodchild (1951). Another significant difference between *A. hylae* and the new species is that the *A. hylae* specimens observed by Goodchild (1951) and Harman & Lawler (1975) had only a rudimentary fossa (where present at all) and none had gills. It is possible that *A. hylae* would develop gills in a free-living state, but no specimens of this species have ever been found outside of the frog hosts, despite a search in ponds frequented by the frogs (Harman & Lawler, 1975). The only other *Allodero* known to have gills within the branchial fossa is *A. lutzi* of South America which has four pairs, as opposed to the two pairs of *A. litoria*. In *A. lutzi*, the gills are lost when the worms are within the frogs. Neither gills nor papillae have been reported for the remaining three species (*A. bauchiensis*, *A. floridiana* and *A. malayana*). Only a few specimens of the new species had fossa and gills which may indicate they had been within the frogs for a shorter period.

The apparently incomplete alimentary canal of many *A. litoria* specimens has also been noted for all other commensal species of *Allodero*, including *A. hylae* (Goodchild, 1951), *A. bauchiensis* (Stephenson, 1930), Brazilian specimens of *A. lutzi* (Michaelsen, 1926b) and *A. floridiana* (Harman, 1971). This suggests that the worms do not ingest food while in the frog hosts, although Stephenson (1930) suggested that *A. bauchiensis* absorbed secretions of the frogs lachrymal gland through its body wall. Gelder (1980), in a review of oligochaete associations, discussed what is known of *Allodero* feeding biology, but did not mention the chlorogogue tissue surrounding the intestine that is particularly abundant in many *Allodero*, compared to other *Dero* and other Naididae. This tissue, which often fills the coelomic cavity of *Allodero*, is known to be involved in storage and metabolism of glycogen and lipids (Jamieson, 1981). The worms may use the chlorogogue tissue to build up an energy store while feeding outside of their hosts: the gut then degenerating when the worms are inhabiting the frogs. At least one species, *A. lutzi*, is known to occur outside of its frog hosts, in aquatic habitats, where it develops gills and dorsal hairs and presumably then feeds in the normal way. How and when the worms find and enter new hosts is not known. Non-commensal *Dero* are all aquatic and frogs may be infected when in water, which they enter to lay eggs.

The frogs, which were subjectively judged by the farmer to be thin compared to the general popula-



FIG. 3. Cross section through *L. caerulea* Wolffian duct with enclosed specimen of *A. litoria* sp. nov.

tion, had a mean body length (SVL) of 8.0cm, ranging from 6.5 to 10cm. The new species of *Allodero* was found associated with slight to moderate dilatation of one or both Wolffian ducts in 12 frogs. The number of worms removed from the ducts of each frog is as follows (with the number of frogs in parentheses): 1(1), 2(2), 3(2), 5(1), 6(1), 10(1), 11(1), 12(1), 15(1), and 23(1). The cloacas were not examined. While the ducts were being dissected, the oligochaetes were observed to actively move to the proximal portions adjacent to the kidneys. The worms appeared to be approximately evenly distributed between left and right ducts.

Most of the 52 frogs submitted for examination were thin and had depleted fat bodies. Regardless of the presence or absence of oligochaetes no inflammatory or degenerative lesions were detected on histopathological examination of the kidneys and Wolffian ducts (Figs 3, 4). Histological examination of other organs revealed inflammatory lesions in the livers of 34 frogs, with the

most severe forms associated with the presence of *Myxidium* trophozoites in the hepatic ducts (Hill et al., 1997). The livers of the 12 frogs which harboured oligochaetes in their Wolffian ducts were normal in four frogs while the remainder had hepatitis of varying severity.

Apart from possible partial obstruction of the Wolffian ducts this new species of *Allodero* appears to have no adverse effect on the host. In this respect it is similar to the other endosymbiont oligochaetes, *A. lutzii* (Michaelsen, 1926a) and *A. hylae* (Goodchild, 1951), described in the Wolffian ducts of the amphibian genus *Hyla*. Following the discovery by Markiw & Wolf (1983) that *Myxosoma cerebrealis*, the agent of salmonid whirling disease, required a tubificid worm in its life cycle, Delvinquier (1986) speculated that *Myxidium* in amphibians may also require a similar intermediate host. Whether any relationship exists between the new species of oligochaete described here and the *Myxidium* described by Hill et al. (1997) is presently unknown but is under investigation.

ACKNOWLEDGEMENTS

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FIG. 4. Cross section through *L. caerulea* kidney and Wolffian duct with enclosed specimen of *A. litoria* sp. nov.

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OBSERVATIONS ON A LARGE POPULATION OF THE VULNERABLE PYGOPODID, *DELMA TORQUATA*.

ROBERT PORTER

Porter, R. 1998 06 29: Observations on a large population of the vulnerable pygopodid, *Delma torquata*. *Memoirs of the Queensland Museum* 42(2): 565-572. Brisbane. ISSN 0079-8835.

The pygopodid, *Delma torquata*, is listed by ANZECC (1991) as vulnerable. The current study shows that, despite the paucity of previous records, the species can be relatively abundant at localities of suitable, undisturbed habitat. The density of this population appears to differ markedly from that observed for other *Delma* spp. Field data indicate that this species is a diurnal, thigmothermic, insectivore whose occurrence suggests a preference for rocks of slightly larger than average size, situated amongst sparsely vegetated areas. Juveniles attain a snout-vent length of 32mm by their first winter. This size is doubled by the third winter. The species' apparent sensitivity to minor habitat disturbance or alteration may be a contributing factor to its scarcity and patchy distribution. □ *Pygopodidae*, *Delma torquata*, vulnerable, population study, southeast Queensland.

R. Porter, Australian Reptile Park, P.O. Box 192, Gosford, New South Wales 2250, Australia; 18 May 1997.

To date, *Delma torquata* Kluge, 1974 is restricted to 13 scattered localities in SE Queensland (Kluge, 1974; Ingram & Raven, 1991; Queensland Museum records). It is currently listed as vulnerable (ANZECC, 1991). A contributing factor, to this status is that much of its distribution coincides with areas of high human population and impact (Czechura & Covacevich, 1985). This apparent rarity is also reflected by the small number of specimens currently held in Australian museums (Queensland Museum, [13] QMJ5683, 9285, 14365, 21220, 21667, 22026, 25997, 27520, 31592, 40346, 41366, 49250, 56999; Australian Museum, [1] AMR12611).

The aim of this study was to collect basic ecological data for this species, which could then be used for a more intensive analysis of the species' life history. This information could be incorporated into conservation management plans in an attempt to safeguard this lizard's future survival.

STUDY SITE

On Brisbane City Council land in the Mt Crosby area, 30km W of Brisbane city, an area was chosen where a handful of specimens had been located (27°31'44"S 152°48'46"E). After two visits, it was apparent that *D. torquata* was present at four separate rocky sites. One main study site was chosen ('West') with two auxiliary sites as backup ('East' and 'Top'). 'West' was situated on the western side of a rocky ridge which is bisected by a dirt track. The site

measured approximately 100m long, parallel to the ridge, and 30m wide down the western slope. It contained many small scattered loose rocks up to 700mm in diameter, plus some areas of exposed bedrock outcrops (Fig.1). The gradient averaged around 30° (range 0-50°). The other two sites were similar, 'East' being on the opposite side of the same ridge as 'West', 'Top' on the crest of a different ridge some 1500m to the south.

The area supports open, dry eucalypt woodland dominated by *Eucalyptus crebra*, *E. intermedius* and *E. maculata*, with an understorey of native and introduced plants and ground covers, particularly the introduced *Lantana montividenensis* and the grasses *Cymbopogon refractus*, *Heteropogon contortus* and *Themeda triandra*. The substrate is covered in a 5-20mm layer of dry leaf litter. Soils are shallow and stony, and comprise poor quality lithosols on the ridges, with texture contrast soils on the slopes. Rocks are mostly mixed metamorphics of the Nerrenleigh-Fernvale beds which include mudstones, chert, jasper, shale, basic volcanics and possibly laterites, although the latter are usually associated with higher altitudes (B. Powell, pers. comm.).

The average annual rainfall recorded at the Mt Crosby water treatment plant, 2km from the study site, over the last five years was 824mm (Brisbane City Council records). Most rainfall occurred between Dec. and March. Temperatures recorded over the last three years for Mt Crosby (5km from the study site), range from 1.0-41.5°C. (pers. obs.).



FIG. 1. *Delma torquata* habitat in 'West' study site, Mt Crosby.

METHODS

Initially, the study sites were visited once per month (June–Oct., 1993). Specimens were located by rock turning. For each capture site the following details were recorded; capture time and date; air temperature and humidity; under rock temperature; cloud cover; capture rock size; aspect and gradient; percentage rock and vegetation cover in a 2×2 m quadrat around the capture rock; plant species in the same quadrat; distance and bearing from a set datum point.

Data concerning the mean rock diameter, percentage rock cover and percentage vegetation cover for the total site were obtained by running five transect lines (three of 50m and two of 30m) approximately 5m apart through the site. Data was recorded at each 2m interval along these lines using a 1×1 m quadrat.

Each specimen was held overnight to facilitate the production and collection of faecal pellets. The following day the lizard was weighed and total length, snout-vent length and tail measurements were obtained by allowing the animal to crawl into a clear (5mm) plastic drinking straw.

This could then be aligned next to a ruler providing measurements to ± 1.0 mm.

Specimens were identified by utilising the throat marbling patterns, which appear to be unique between individuals. A permanent record was obtained by producing a photocopy of the ventral surface of each animal using the 200% enlargement setting.

The photocopy also allowed accurate counting of the paired ventral body scales of each specimen to access sexual dimorphism. These were counted as per Coulson (1990), starting at the first pair of enlarged ventral scales behind the smaller gular scales and ending at the pre-anal scale.

Monitoring the initial five captures after this process did not seem to produce any detrimental effects from the photocopying, and all lizards were subsequently released at the point of capture the following day.

The difficulty of relocating animals on previously searched sites suggested that rock turning may detrimentally alter the microhabitat. The loose substrate often collapsed into the depression vacated by the rock. This theory was reinforced by the ease of locating new specimens on

previously undisturbed sites nearby. Few specimens were located on disturbed sites for at least three months after the initial rock turning.

Consequently, four sets of five pitfall traps were installed in Nov., 1993. Traps were spaced at 1m intervals and comprised four litre plastic buckets dug into the ground flush to the soil surface. Aluminium insect mesh 5m long and 200mm high was used as a drift fence.

Two trap lines were set in a rocky area within the West site and two in a vegetated area with no rocks, some 20m from the nearest rocky area, to the south of East site. One trap line in each area was set parallel to the gradient, the other perpendicular. Traps were opened for 14 days and checked each morning and night, and then closed for six weeks by replacing the bucket's lid. This routine continued from Dec., 1993 until Dec., 1994. Any specimens captured in the traps were processed as previously described.

A final rock-turning survey was carried out at the end of the trapping program to ascertain if specimens had returned to the original area, subsequent to the initial disturbance.

Faecal pellets collected from captured specimens were soaked in 75% alcohol before being teased apart beneath a microscope for identification of material to the lowest possible taxonomic level.

A public awareness campaign was initiated in the southern part of the species' range in an attempt to enlist public assistance with finding new species localities in this area. Photographs highlighting the diagnostic characters were released in both widely distributed and localised newspaper publications (e.g., Brisbane Courier Mail; Karana Kronicle).

RESULTS

Thirty-nine specimens were captured and identified; 27 from West, 6 from East and 6 from Top. Two animals were recaptured once, one each from West and East, and one specimen from West was recaptured on two occasions (once beneath a different rock after 28 days and 3.5m from the original capture site, and again after 427 days another 18.2m from the second capture point). The two single recaptures were each located under the same rock as the original capture after periods of 33 and 28 days.

All hand captures during the study were found under rocks, with the exception of one specimen which was observed actively moving amongst low grasses at 08:45 hours on 8 Dec., 1992 at an air temperature of 26°C. Many specimens were

extremely quick when disturbed beneath rocks and several evaded capture (one escaped into a termite burrow), suggesting the lizards were quite active before capture. All specimens were found on the surface of the soil usually with dorsal contact to the rock above, although one was located beneath a rock curled within a chamber of a subterranean termite nest.

Specimens were located beneath rocks during every season of the year. One was located for every 1.75 hours of searching regardless of season. This equates to around one lizard for every 150-200 rocks lifted.

The final rock-turning survey at the end of the pitfall trapping program produced a total of eight specimens of *D. torquata* over the entire West site during ten search hours. This equals the maximum number of specimens located in one day during previous visits, indicating the habitat had not been permanently damaged, although none of these eight were recaptures.

Only six captures were made in pitfall traps over the trapping period, four in Dec., one in Feb. and one in October. All were found in traps when they were checked in the afternoon, indicating activity and capture between 06:30-17:00 hours. Specimens of *D. torquata* were caught in both trap lines in the rocky area (four specimens) and in one trap line in the vegetated site (two specimens). A total of 1,960 trap days were carried out over the 13 month period to produce a success rate of 0.306 animals per 100 trap days.

Snout-vent length (SVL), tail length, weight and ventral scale count were recorded for each individual (Table 1). SVL's ranged from 31-70mm with a maximum total length of 196mm and a maximum weight of 1.78g. The smallest specimen found (SVL 30mm; mass 0.23gm) was located on the 3 Aug., 1993, while another captured on 4 Oct., 1994 measured 31mm SVL and weighed only 0.19g.

It was difficult to ascertain if tails were original or regrown, as the latter rarely exhibited an obvious demarcation point. Intact tails appeared to measure around 200% of the body length, with a maximum recorded at 214%. An arbitrary length of greater than 180% was chosen to indicate an intact tail in this study, which provides a figure of 66% of the population with regenerated tails.

Some indication of microhabitat use emerged. The diameter of rocks utilised by the lizards (mean 172cm) was significantly different to that of the whole study area where the mean was 126cm ($t_{143}=2.48$, $P=0.014$). Similarly, a significant

difference was found between the percentage vegetation cover for the study area (mean 42%) and the capture points (mean 31%), ($t_{139}=2.25$, $P=0.026$). Mean percentage rock cover for the study area (27%) was not significantly different to that for the capture points (33%), ($t_{141}=1.25$, $P=0.21$). Microhabitat temperatures varied greatly compared to ambient air temperatures, ranging from 8.8°C below ambient to 4.1°C above. The mean difference was 1.7°C below ambient for 34 captures.

As only 14 museum specimens were available, it was not possible to ascertain if ventral scale numbers are sex-linked in *D. torquata* without sacrificing living specimens. This did not seem justifiable for the present study. The degree of overlap of ventral scale counts between the sexes has inherent problems in accurately determining sex in many individuals. Handley (1994) showed that the only positive method of sexing *D. impar* Fischer, 1882 is to analyse X-rays of individual lizards to establish if a pair of post-cloacal bones are present or absent, as these only occur in males. X-ray facilities were not available during this study.

Contents of 14 faecal pellets collected from specimens at the Mt Crosby site were recorded (Table 2). Thirteen of 14 pellets contained insect or spider remains, mostly small cockroaches which were present in at least 8 of 14 pellets.

DISCUSSION

DISTRIBUTION AND HABITAT. The public awareness campaign produced no confirmed new locality records for *Delma torquata*. One tentative record was obtained from the Kalpowar area (24°42'S 151°19'E).

The previously described habitat of dry open eucalypt/*Acacia* woodland, with a sparse understorey of native grasses and small shrubs, usually associated with rocky outcrops on ridges (Wilson & Knowles, 1988) was confirmed in the present study. The requirement for rocky sites may be a biased perception caused by the problems of locating a small, agile lizard amongst vegetation. In the current study, specimens were located in pitfall traps up to 20m from the nearest rocks.

The holotype was found in black basalt soil six inches below the surface during posthole digging (Kluge, 1974). This observation has prompted previous authors to speculate that the species is a burrower (e.g., Cogger, 1992). However, Wilson & Knowles (1988) indicated otherwise and data from the current study show that this species is an active surface forager, as suggested by these authors.

POPULATION AND GROWTH. The small number of animals recaptured during this study and the apparent disturbance of animals by rock turning, violates the mark-recapture technique's assumption of constant trapability (Seber, 1973). Thus, it was not possible to accurately calculate an estimate of population size of *D. torquata* at the Mt Crosby study site. This problem is further exacerbated by sampling being only possible in the rocky areas of the site despite evidence from pitfall traps that other areas are utilised.

It is possible to surmise that the Mt Crosby population is relatively large, given the number of animals found and the small number of recaptures, with new captures still being made at the termination of the study; that the species is widespread because specimens were found at all rock outcrops examined and may be more widely distributed depending on their use of vegetated areas; that it is reproductively active, several juveniles being located during the study, their sizes being comparable to a hatchling (SVL 28mm) obtained from an egg (Kluge, 1974); and that it is apparently healthy, as all individuals appeared to be in good condition.

The data enable tentative prediction on the presence of size cohorts within the study population (Figs 2 & 3). A first winter cohort averages 32mm SVL and a mass of 0.28g ($n=4$). The second cohort is identifiable at a mean SVL of 52.6mm and 0.91g ($n=14$). A third cohort is less evident but seems to be present around 65mm SVL ($n=5$) and 1.41g ($n=4$).

The proportion of animals showing autotomy in this study is relatively high compared to two studies of *D. impar* (Coulson, 1990; Kutt, 1992). Coulson (1990) found the incidence of autotomy varied greatly from site to site, ranging from zero ($n=13$) at Rockbank to 57% at Derrimut. His analysis also showed that this difference was significant and postulated the cause as being differential levels of predation. Kutt's (1992) data indicated autotomy in 39% of the population. The 66% figure in the current study may be artificially high due to the difficulties of distinguishing whether specimens had original or regrown tails. It is possible that autotomy is related to the occurrence of intraspecific aggression rather than just predation. Agonistic interactions have been recorded in other *Delma* species, e.g., *D. inornata* Kluge, 1974 and *D. tinctoria* De Vis, 1888 (Sonne-man, 1974, and pers. obs.).

HABITAT UTILISATION. The statistically significant results obtained concerning microhabitat utilisation suggest that *D. torquata* has a preference

TABLE 1. Body and tail measurements, mass and ventral scale counts of *D. torquata* specimens at Mt Crosby. * denotes recapture.

Date	Specimen No.	SVL (mm)	Tail (mm)	Tail/SVL (%)	Mass (gm)	Ventral Scale No.
3/6/93	T1	49	36	196	0.92	57
3/6/93	T2	31	63	203	0.32	61
3/6/93	T3	33	52	158	0.29	62
3/6/93	W4	61	114	187	1.41	60
3/6/93	W5	57	100	100	1.14	65
3/6/93	W4	45	87	193	0.66	58
3/6/93	W7	54	54	100	0.97	61
6/7/93	T1	61	51	100	0.68	62
6/7/93	W4	54	70	130	0.66	62
6/7/93	W6*	45	49	220	0.64	58
3/8/93	T10	61	100	214	1.04	60
3/8/93	I33	33	59	173	0.28	61
3/6/93	W12	60	60	100	1.1	60
3/8/93	W13	70	103	147	1.27	60
3/6/93	W13	65	114	103	1.45	62
3/8/93	W15	56	36	60	0.71	62
3/8/93	W16	49	54	114	0.75	60
3/8/93	W17	36	61	170	0.23	60
7/9/93	W18	52	100	210	0.97	60
7/9/93	W19	49	45	92	0.65	60
7/9/93	E20	53	100	200	1.09	60
7/9/93	E21	60	58	133	1.51	63
7/9/93	E22	58	115	100	1.27	54
7/9/93	E23	62	85	137		62
5/10/93	W24	55	112	204	1.14	60
5/10/93	W25	49	69	141	0.77	58
5/10/93	E20*	53	100	204	1.17	60
5/10/93	W19*	49	47	36	0.73	60
12/12/93	E26	52	103	100	0.95	54
17/12/93	W27	54	114	100	1.22	62
20/12/93	W28	49	60	196	0.83	60
10/2/94	E29	45	41	41	0.46	61
15/2/94	W30	49	54	103	0.65	60
4/10/94	W31	31	47	152	0.19	58
5/12/94	W19*	52	70	146	0.76	60
4/4/95	W32	70	126	100	1.78	62
4/4/95	W33	52	60	162	0.8	60
4/4/95	W31	36	52	173	0.64	58
4/4/95	W35	49	87	170	0.64	62
4/4/95	W36	53	100	200	0.97	60
4/4/95	W37	47	69	147	0.74	61
4/4/95	W38	45	90	200	0.70	60
4/4/95	W39	50	85	170	0.65	59

for parts of its habitat. Slightly larger than average rocks are chosen, usually with less than average associated vegetation cover. This pattern may be related to the thermoregulation requirements of this lizard. These rocks may heat faster, with less shade from vegetation, while cooling down slower because of the greater mass to surface area ratio.

An inference from this study was the apparent sensitivity of *D. torquata* to habitat disturbance. It is uncertain if this adverse reaction was in

response to habitat modification caused by rock turning, a stress reaction caused by the trauma of capture and processing, or a combination of the two.

Kutt (1992) captured 115 specimens of *D. impar*. Despite removing specimens from the site for processing and marking by heat-branding, one third of those were recaptures, indicating that pitfall trapping and handling do not preclude recapture. The specimens re-located in the present study at the disturbed site some 20 months after the last rock turning exercise does indicate that, if initial habitat alteration was a problem, it did not have a lasting detrimental effect.

Such sensitivity may explain the patchy distribution of the species. However, it does not provide answers as to why *D. torquata* is apparently still uncommon in some of these undisturbed sites, e.g., Crow's Nest NP where only one specimen has been recorded (Queensland Museum records). This may relate to insufficient surveying of these sites in the past, or their lack of optimal habitat.

The inefficiency of the pitfall traps is probably attributable to both the relatively low overall density of the species and to the problems of installing traps precisely enough to stop a 3-4mm diameter animal passing beneath the drift fence. This problem was further compounded by the steep gradient of the site, which was prone to erosion around the traps and fencelines.

Despite the apparent trap inefficiency, the trapping success rate in this study of 0.306 animals per 100 trap days is comparable to the figure of 0.304 animals obtained by Kutt (1992) working with *D. impar*. Captures in pitfall traps in both rocky and vegetated areas suggest the use of both habitats by *D. torquata*. It is still uncertain if specimens are commuting between these habitats, or if some lizards remain in each particular habitat for extended periods.

TABLE 2. Food items identified in faecal pellets from specimens of *D. torquata* captured at Mt Crosby.

Specimen No.	Date	Items Identified in Faecal Pellets
-	8/12/92	Family Blattellidae - fragments
-	8/12/92	Family Blattellidae - fragments
-	8/12/92	Family Blattellidae - fragments
T1	5/6/93	Plant matter - one piece
T2	5/6/93	Class Insecta - mandible ?coleopteran larvae
T3	5/6/93	Family Blattellidae - fragments
W9	7/7/93	Class Insecta - setae and cuticle
W19	7/9/93	Family Blattellidae - fragments
E36	7/9/93	Family Blattellidae - fragments
-	7/9/93	Class Insecta - leg segments
W22	17/12/93	Order Araneidae - fragments
W23	21/12/93	Family Blattellidae - fragments
-	10/2/94	Family Blattellidae - fragments
W24	15/2/94	Class Insecta - setae

Coulson (1990) indicates a similar possibility with *D. impar*, which were also initially only found under rocks. He states 'surveying reptiles by turning rocks has undoubtedly led to a biased perception of the significance of rocks as an essential habitat requirement, since the striped legless lizard is clearly not confined to rocky areas'. Coulson also points out that the presence of rocks often precludes the clearing and cultivation of native grasslands which, when other non-rocky areas are cleared, confines the species to these rocky sites, giving an unrealistic impression of the species' distribution.

The Mt Crosby study site has apparently never been cleared of vegetation and has only been affected by occasional natural fires (J. Hester, pers. comm.). Consequently, disturbance to the area has been kept to a minimum, which may explain the presence of relatively large numbers of *D. torquata*. Specimens still occur in disturbed areas around the site but the density appears much lower (pers. obs.).

ACTIVITY AND BEHAVIOUR. The pitfall trapping in this study also provided invaluable data concerning the activity patterns of the species (i.e., diurnally active), at least during certain times of the year. Pygopodids have often been regarded as being mostly nocturnal or crepuscular (Worrell, 1963; Kluge, 1976), including *Delma* species (Patchell & Shine, 1986). Personal observations of both *D. tinctoria* and *D. inornata* in captivity also indicate diurnal activity periods.

It is possible that activity cycles may be effected by the prevailing weather conditions. Jenkins & Bartell (1980) noted nocturnal and crepuscular

activity for *D. impar* on hot days, whereas field research recorded diurnal activity (Coulson, 1990). Kutt (1992) found the day time to be the primary activity period for the species, with 17 of 26 captures made during the day. The time of capture of the remaining lizards could not be determined.

The thigmothermic behaviour of some *Delma* species, e.g., *D. impar* (Coulson, 1990), may give the impression of diurnal inactivity, as the animals are thermoregulating indirectly beneath rocks, etc. between periods of activity. This phenomenon appears to be present in *D. torquata*, as specimens disturbed beneath rocks were often extremely quick and evasive, perhaps indicating that they had been active previously and were attempting to re-adjust their body temperatures.

That *D. torquata* is susceptible to pitfall trapping suggests that the species is an active surface forager rather than a fossorial or burrowing species, as has been postulated in the past (Cogger, 1992; Ehmann, 1992). However, a burrowing habit does not necessarily preclude pitfall susceptibility as other such species, such as *Aprasia* and *Lerista*, are often caught in this fashion (G. Shea, pers. comm.). The finding of the type specimen underground (Kluge, 1974) does indicate some subterranean habits, perhaps associated with winter inactivity.

The two recaptures of specimens of *D. torquata* beneath the same rock after periods of around a month suggest the use of a specific home site. The second recapture of a specimen after 427 days only 18.2m from its previous location also hints at a potentially small home range. However, the lack of recaptures may also be interpreted as an indication of a highly mobile species. A similar dearth of recaptures was found in two separate studies of *D. impar* (Coulson, 1990; Moro, 1990).

The production of faecal pellets by several specimens captured in mid-winter (June and July), is indicative of feeding activity at this time, possibly inferring that the species does not obligatively enter a winter dormant phase. Pitfall captures only occurred from spring through to late summer, which may indicate at least a partial reduction of activity over winter. Other researchers have expressed difficulty in finding specimens of *D. torquata* after prolonged dry spells (S. Wilson, pers. comm.). That observation was not supported by the present study, specimens being found throughout winter and spring 1993, one of the driest on record for Brisbane (total annual rainfall at the Mt Crosby water treatment plant was only 582mm).

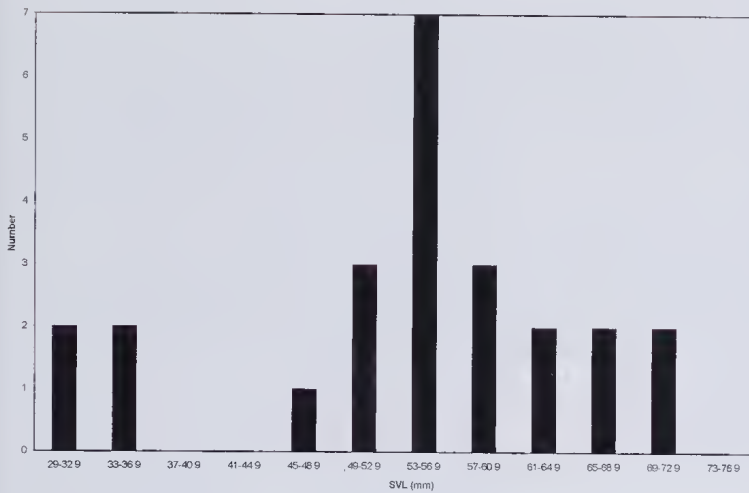


FIG. 2. Snout-vent lengths (mm) of all individual *D. torquata* captured during winter (June-Aug.) at Mt Crosby.

The indication that the microhabitat temperatures utilised by *D. torquata* were lower on average than the ambient air temperature is probably an artefact of the majority of the surveying being carried out between 07:00-12:00 hours, before direct solar radiation has had a major effect on heating the rocks concerned. That many lizards appeared very active when uncovered beneath rocks may suggest that they had already attained a preferred body temperature elsewhere and had subsequently moved beneath the rock.

DIET. Kutt (1992) found *D. impar* was more likely to defecate when cooled for 5-10 minutes in a refrigerator. This did not appear to be the case with *D. torquata*. The small number of pellets obtained does not provide a full picture of the diet of this species, but it does indicate that it is an insectivore with a possible preference for small cockroaches (Table 2).

These data agree with Patchell & Shine (1986). The three *Delma* species studied (*D. inornata*, *D. fraseri* Gray, 1831 and *D. nasuta* Kluge, 1974) were all active terrestrial foragers with generalised insectivorous habits, hunting mainly on the surface for active insects. Coulson's (1990) results from analysis of *D. impar* pellets were similar to that found in this study, in that the diet was generalised, but with a

suggested preference towards one particular prey type — noctuid moth larvae.

STATUS. The apparent rarity of *D. torquata* may be a true indication of its status, not merely a reflection of its small size and secretive nature. Taking the Mt. Crosby site as an example of a natural population size and density, it appears that, where it does occur on undisturbed sites, the species is relatively abundant. These population characteristics seem to differ from some other species of *Delma*, e.g., *D. plebeia* De Vis, 1888 and *D. tincta*. Despite being common and widespread, these species

can be difficult to locate (P. Couper and S. Wilson, pers. comm. and pers. obs.).

The scarcity of *D. torquata* in museum collections is further emphasised by the lack of public feedback received from the public awareness campaign initiated with this study. Approximately 30 telephone calls and letters were received following the press releases and of these only one was a potential sighting.

The indication that *D. torquata* is sensitive to even minimal habitat disturbance should be investigated more thoroughly. It is possible that land clearing and modification may be the most important factor dictating the current distribution

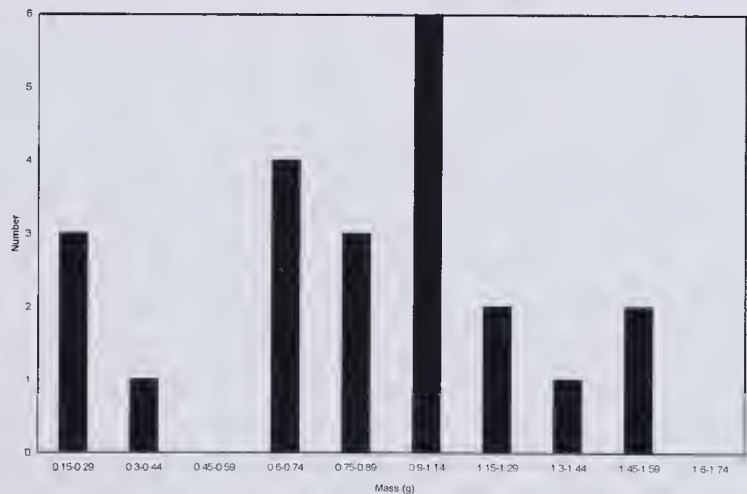


FIG. 3. Mass (g) of all individual *D. torquata* captured during winter (June-Aug.) at Mt Crosby.

of this species as seems to be the case with certain other pygopod species, e.g., *D. impar*, *Paradelma orientalis* (Günther, 1876) and *Pletholax gracilis* Cope, 1864 (Coulson, 1990; Ehmann, 1992).

A draft recovery plan for *D. torquata* has been produced by the Queensland Dept of Environment and Heritage (now Qld Dept of Environment) (C. Davidson pers. comm.), with an emphasis on surveying other potential areas of habitat and investigating the ecology of the species. The most important outcome of the current study in this respect is the discovery of a large, healthy population of a vulnerable species. The location of this population on council owned land means these animals should remain undisturbed and secure for the future.

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RECOGNITION OF *EULAMPRUS TRYONI* (LONGMAN), A SCINCID LIZARD
ENDEMIC TO THE McPHERSON RANGES OF EASTERN AUSTRALIA

ROSS A. SADLIER

Sadlier, R.A. 1998 06 29: Recognition of *Eulamprus tryoni* (Longman), a scincid lizard endemic to the McPherson Ranges of eastern Australia. *Memoirs of the Queensland Museum* 42(2): 573-578. Brisbane. ISSN0079-8835.

Lygosoma (Hinulia) tryoni Longman is resurrected from the synonymy of *Eulamprus murrayi* (Boulenger) as *Eulamprus tryoni* (Longman) new. comb. *E. tryoni* is a moderately large skink with a distinctive coloration that features dark bands on the body and dark blotches above the forelimbs and side of the nape. It is restricted to high altitude closed forest on the McPherson Range in northeast New South Wales and southeast Queensland. It is sympatric with *E. murrayi* over at least part of its range. The species' known distribution is entirely within existing reserves and it is not considered to be under any immediate threat.

□ Lizard, Scincidae, *Eulamprus*, McPherson Range, rainforest, conservation.

Ross A. Sadlier, Australian Museum, 6 College Street, Sydney 2000, Australia; 17 April 1998.

In the Border Ranges region of New South Wales (NSW) and Queensland (Qld) two species of ground dwelling skinks similar in size, colouration and habit, occur in sympatry in high altitude closed forest habitat on the Lamington Plateau.

One of these, *Eulamprus murrayi* (Boulenger), is moderately widespread at both a local and regional level. It is distributed throughout closed forests from the Conondale Ranges in the north (26°40'S) to Barrington Tops (32°10'S) in the south, and occurs over a wide altitudinal range throughout much of its distribution. The other species is that described by Heber A. Longman in 1918 as *Lygosoma (Hinulia) tryoni*. Longman's description is based on two specimens collected by Mr Henry Tryon from the 'Macpherson Ranges, 3,000ft., Southern Queensland'. The name was subsequently used by Worrell (1963), as *Lygosoma tryoni*, in an abbreviated description presumably of *E. murrayi* (the description lists characters of both *tryoni* and *murrayi*), and figures a specimen of *E. murrayi*.

In recent times *Lygosoma (Hinulia) tryoni* has been regarded as a synonym of *E. murrayi* (Cogger et al., 1983). However recent work presented here clearly shows the two species are distinct, and Longman's species is here recognised as *Eulamprus tryoni* (Longman).

***Eulamprus tryoni* (Longman)**

MATERIAL. Specimens are lodged in the Australian Museum, Sydney (AMS), Queensland Museum (QM), and Australian National Wildlife Collection, Canberra (ANWC). An asterisk indicates specimens used in compiling Table 1. *Eulamprus tryoni*: AMSR151789*

Border Ranges NP, Evans Falls on Brindle Ck walking track (800m asl), NSW 28°22'S 153°03'E (14/12/1997); AMSR151790*, 151802-03* Border Ranges NP, Silva Falls on Brindle Ck walking track (840m asl), NSW 28°22'S 153°03'E (14/12/1997); AMSR151794-96* Border Ranges NP, Tweed Valley Lookout (1,100m asl), NSW 28°22'S 153°05'E (13/12/1997); QMJ3023* (holotype) Springbrook [= Springbrook], SEQ (Covacevich, 1971) cited as 'Macpherson Ranges, 3,000ft., Southern QLD' by Longman (1918); J22703 Lamington NP, Qld. (27/1/73); QMJ29945 Lamington Mt., O'Reillys, on farm (24/7/73); QMJ64635-38* all from Tooloona Falls Walk, Lamington NP (64635 Yilgahn Falls 1,010m asl; QMJ64636 Tooloona Falls 1,040m asl; J64637 Triple Falls 800m asl; QMJ64638 Chalahn Falls 950m asl); ANWCR5688*, 5695* Border Ranges NP, Paddys Mountain Rd (site 32), NSW 28°25'02"S 153°25'02"E. *Eulamprus murrayi*: AMSR1517801-02* Border Ranges NP, vic. Silva Falls on Brindle Ck walking track (840m asl), NSW 28°22'S 153°03'E (14/12/1997); AMSR151791-93* Border Ranges NP, Tweed Valley Lookout (1,100m asl), NSW 28°22'S 153°05'E (13/12/1997); AMSR151785-88* vic. Brindle Ck. walking track (760m asl), NSW 28°22'S x 153°03'E (14/12/1997); QMJ64639-41* all from Tooloona Falls walk, Lamington NP (64639-40 Picnic Rock 900m asl; QMJ64641 Tooloona Falls 1050m asl); ANWC R5801* Border Ranges NP, Paddys Mountain Rd (site 32), NSW 28°25'02"S 153°25'02"E.

DIAGNOSIS. *Eulamprus tryoni* is readily distinguished from other members of the genus by the following combination of characters: upper labials 6; last upper labial scale divided by an oblique longitudinal suture (Fig. 1); midbody scale rows 38-42; dorsal scale rows 81-92; lateral surface featuring a large black shoulder patch;

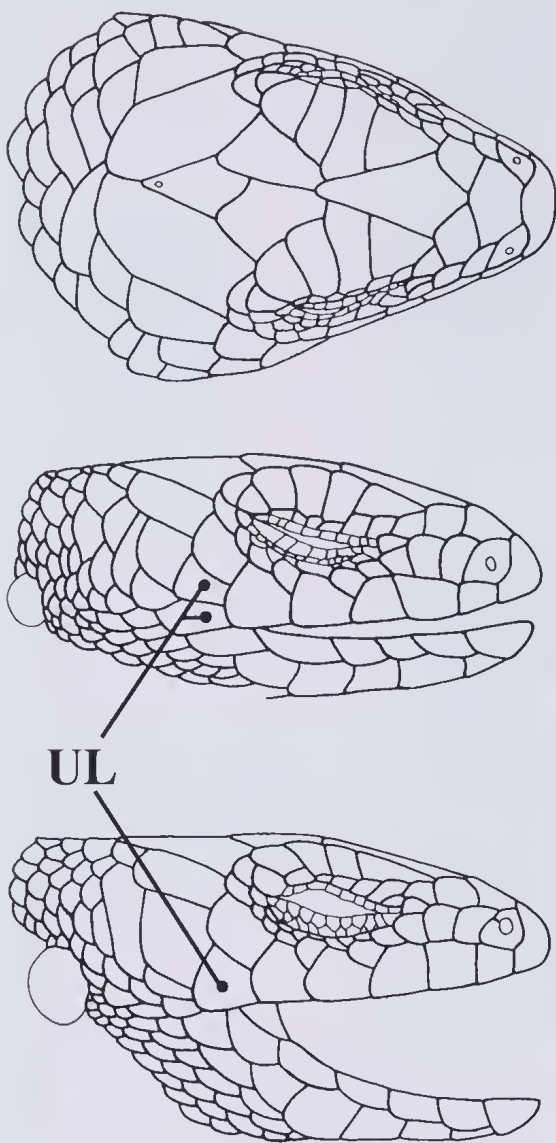


FIG. 1. A, dorsal and B, lateral headshields of *E. tryoni* (QMJ3023). C, lateral headshields of *E. murrayi* (AMR151802); note divided last upper labial (UL) in *E. tryoni* and single upper labial in *E. murrayi*.

ventral surface in life with a bold enamel yellow flush from forelimb to tail.

Details of holotype of *Lygosoma (Hinulia) tryoni*: SVL 104mm; tail length 120mm; midbody scale rows 40; dorsal scale rows 84.

DISTRIBUTION. Known only from the Lamington Plateau, the southern and eastern edge of which lies on the NSW/QLD border. The NSW records are all within the Border Ranges NP and the QLD records from within or adjacent to Lam-

TABLE 1. Comparative table of measurements and proportions for *Eulamprus tryoni* and *Eulamprus murrayi* based on samples from regionally sympatric populations. Abbreviations (body measurements are expressed as percentages of snout to vent length): SVL=snout to vent length - measured from tip of snout to caudal edge of anal scales; AG=axilla to groin distance - measured from middle of base of forelimb to middle of base of hindlimb; FL=forelimb to snout length - measured from tip of snout to middle of base of the forelimb; HL=hindlimb length - measured from middle of base of hindlimb to tip of fourth toe including nail; TL=tail length - measured from posterior edge of anal scales to tip of tail, on complete original tails only; MBR=midbody scale rows - number of longitudinal scale rows around body counted midway between fore and hind limbs; DSR=paravertebral scales - number of scales in a paravertebral row from first scale posterior to parietal scale to last scale anterior to level of vent opening; 4FL=fourth finger and 4TL=toe lamellae - number of ventral scales on fourth digit of hand and foot, distal scale contains claw and basal scale is last largely undivided scale at a point level with intersection of third and fourth digits.

	<i>E. tryoni</i>	<i>E. murrayi</i>
Maximum SVL	104mm	108mm
AG range	50.0-58.2	52.4-56.7
mean	54.5	55.2
n	14	14
FS range	35.7-42.2	39.4-42.9
mean	40.1	40.7
n	14	14
HL range	36.5-44.6	34.3-43.3
mean	40.7	38.7
n	14	13
TL range	115.4-130.4	123.7-146.1
mean	122.9	133.2
n	2	4
MBR range	38-42	28-36
mean $\pm$ sd	40.0 $\pm$ 1.11	33.1 $\pm$ 1.87
n	14	14
DRS range	81 - 92	59-67
mean $\pm$ sd	85.9 $\pm$ 2.92	61.8 $\pm$ 2.12
n	14	14
4FL range	11 - 14	11-13
mean $\pm$ sd	12.6 $\pm$ 0.69	12.0 $\pm$ 0.55
n	14	14
4TL range	16-21	16-20
mean $\pm$ sd	18.4 $\pm$ 1.08	18.5 $\pm$ 0.99
n	14	14

ington NP, the straight line distance between these sites being approximately 17km.



FIG. 2. *E. tryoni* from Border Ranges NP, NSW.

BIOLOGY. *E. tryoni* is restricted to closed forest habitat. The specimens collected in the Border Ranges NP in Dec., 1997 were taken during the course of two consecutive afternoons when conditions were warm. All were observed on logs or rocks on the forest floor, but not necessarily in sunlit areas. When disturbed they generally sought shelter under these sites, or within cavities in fallen logs.

Both *E. tryoni* and *E. murrayi* are broadly sympatric at both sites between 800 and 1000+m, and were encountered in relatively low numbers in this altitudinal range. By contrast more than 25 *E. murrayi* were observed along the Brindle Ck trail between 760m and 840m during the course of a two hour (approximately) walk in an afternoon.

The stomach of the holotype has what appears to be amphibian eggs visible through wall of the stomach lining, the quantity indicating the ingestion was not accidental.

COMPARISON WITH OTHER SPECIES. The genus *Eulamprus* as it is currently conceived is an assemblage of *Sphenomorphus* group species characterised by a single derived character state

only — ovoviparity (Greer, 1989). Within *Eulamprus* there are two groups which comprise natural lineages, the *E. quoyi* group and the *E. murrayi* group, the remaining species being essentially an assemblage of taxa not assignable to either group. At the time it was defined (Greer, 1989), the *E. murrayi* group contained the species *E. murrayi* and *E. luteilateralis*, and was differentiated from all other *Eulamprus* by the following suite of derived character states: third pair of enlarged chin scales separated by 5 instead of 3 longitudinal rows of small scales; inguinal fat bodies absent; and postmental contacted by a single upper labial. *Eulamprus tryoni* has all these features and clearly is a member of the *E. murrayi* group.

Eulamprus tryoni and *E. murrayi* are sympatric in high altitude closed forest of the McPherson Ranges. They are similar in overall size and to some extent in coloration, but differ markedly in scalation. *E. tryoni* has more midbody scale rows (38-42 vs 32-36), more dorsal scale rows (81-92 vs 58-67), and the last upper labial is divided (vs single in *E. murrayi*).

In colouration *E. tryoni* (Fig. 2) has a pattern of boldly contrasting and well defined, dark,



FIG. 3. *E. murrayi* from Border Ranges NP, NSW.

transverse markings (often partly broken along their length) on a light to mid brown dorsal surface, whereas sympatric *E. murrayi* (Fig. 3) are usually darker overall and have dark markings of the dorsal surface more irregularly distributed (occasionally forming poorly defined, transverse bars). Both species have several large, black, transverse ellipses along the lateral surface between (and in the region of) the ear opening and forelimb, the largest being positioned above the forelimb. The remainder of the lateral surface to the level of the hindlimb is much paler in *E. tryoni* than *E. murrayi*, and the distribution of pale markings in this region differs between the two species. Between the fore and hindlimb of the lateral surface *E. tryoni* has a pattern of scattered light and dark scales, with a series of smaller, variably defined dark ellipses along the dorsolateral edge (continuous with dark transverse markings of dorsal surface). In *E. murrayi* this region is dark overall (most concentrated in the area around the forelimb) and has a pattern of numerous, minute, pale spots (usually one or more to each scale). Both species have a yellow flush to the ventral surface in life in the region between the fore and hindlimbs. In *E. tryoni* this is a bold enamel

yellow, whereas in *E. murrayi* it is a pale yellow wash. Both species have dark markings on the throat and along the sutures of the chinshields and mental scales (Fig. 4). The throat markings of *E. tryoni* are obscure, elongate, transverse or longitudinally aligned dark blotches, and the chinshields and mental scales have a narrow dark edging to each scale along the sutures. By contrast *E. murrayi* has extensive dark markings to the chest which tend to align obliquely, and the chinshields and mental scales of the throat have a broad and conspicuous, dark edging to each scale.

Eulamprus luteilateralis, the other member of the *E. murrayi* group, is restricted to closed forest habitat in mid-east Qld. It is unlikely to be confused with *E. tryoni*, being slightly smaller in size (maximum SVL 87mm, Covacevich & McDonald, 1980) than *E. tryoni* (maximum SVL 104mm), lacking the diagnostic divided last upper labial, showing a bright orange lateral surface between the fore and hindlimbs (Covacevich & McDonald, 1980), and in lacking any distinctive dark markings on the dorsal or upper lateral surface, outside of a prominent black shoulder patch.



FIG. 4. Throat colour of sympatric *E. murrayi* (left) and *E. tryoni* (right) from Border Ranges NP, NSW.

E. tryoni is also regionally sympatric with *Eulamprus tenuis*. The two species share a similar colouration of a light background colour with contrasting dark, transverse markings, however, *E. tryoni* is readily distinguished from *E. tenuis* by having: fewer upper labials (6 vs 7); a divided vs single last upper labial; postmental contacted by first upper labial only (vs first & second); and more midbody scale rows (38-42 vs 28-34).

CONSERVATION STATUS. *Eulamprus tryoni* is known only from a relatively narrow belt of high altitude forest on the McPherson Ranges, and as such it has one of the most restricted distributions among the rainforest dependant reptile species of this region. All known records are from within areas reserved as national parks and the species is not considered to be under any immediate threat from development. However, its limited distribution indicates very narrow or specialised habitat preferences. Therefore any proposed change in government policy to open reserve areas for utilisation that results in disturbance to the species preferred habitat could have a significant impact upon it. Less clearly understood are the implications of global climate

warming on a species restricted to high altitude habitats, but an obvious consequence could be a reduction in the lower altitudinal limits of the species, thereby contracting its range and fragmenting now continuous populations.

REMARKS. The description of *Lygosoma murrayi* by Boulenger, 1887 (p. 232) gives 34 smooth scales around the middle of the body and provides an illustration (pl. 13, fig. 1) which is clearly identifiable as what is currently regarded as *E. murrayi*. The only other synonym of *E. murrayi* which predates Longman's description of *Lygosoma tryoni* is *Lygosoma tamburinese* by Lönnberg & Andersson in 1915. This description gives 32 scales around the middle of the body and the throat and chest marbled with dark grey. These characters indicate that *Lygosoma tamburinese* is not conspecific with *E. tryoni*.

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SAPROSCINCUS ORIARUS, A NEW SCINCID LIZARD (LACERTILIA: SCINCIDAE)
FROM THE NORTH COAST OF NEW SOUTH WALES

ROSS A. SADLIER

Sadlier, R.A. 1998 06 29: *Saproscincus oriarus*, a new scincid lizard (Lacertilia: Scincidae) from the north coast of New South Wales, Australia. *Memoirs of the Queensland Museum* 42(2): 579-583. Brisbane. ISSN0079-8835.

Saproscincus oriarus is described from 10 specimens from 5 scattered areas on the north coast of New South Wales. The species is small and most similar to *Saproscincus mustelinus*. It is characterised by a fine white midlateral stripe in both sexes; this character is otherwise present within *Saproscincus* in low frequencies only in females of *S. challengerii*, *S. rosei* and *S. spectabilis*. □ *Scincidae*, *Saproscincus*, *New South Wales*, *coastal*.

Ross A. Sadlier, Australian Museum, 6 College Street, Sydney 2000, Australia; 17 April 1998.

Over the past decade, specimens of a small undescribed species of skink have been deposited in the Herpetology collection of the Australian Museum. These have come from various sources, the majority being collected as voucher specimens during the course of fauna survey work on the far north coast of NSW. The species has been collected from the Myall Lakes area in the south to Byron Bay in the north, in coastal or near coastal habitats, including both artificial and disturbed environments.

The conservation status of *S. oriarus* is unclear. It has an apparently broad distribution but is known from relatively few individuals at any location. Its occurrence in areas altered by human activity indicates that it can persist in disturbed habitat. However, the scarcity of records in one of the most developed regions of Australia also indicates that it may be limited in distribution at a local scale by factors other than habitat type.

Specimens are lodged in the Australian Museum, Sydney (AMS).

MATERIALS AND METHODS

MEASUREMENTS. The following characters were scored for each specimen where possible: snout to vent length (SVL) - measured from tip of snout to caudal edge of anal scales; axilla to groin distance - measured from middle of base of fore limb to middle of base of hindlimb; forelimb to snout length - measured from tip of snout to middle of base of forelimb; hindlimb length - measured from middle of base of hindlimb to tip of fourth toe including nail; tail length (TL) - measured from posterior edge of anal scales to tip of tail, on complete original tails only as determined by x-rays. Body measurements are expressed

as percentages of snout to vent length (SVL) in the taxon account.

SCALATION. Head scalation generally follows Taylor (1935), except for the shields bordering the anterior and lower edge of the eye which follow Sadlier (1986: Fig. 2); midbody scale rows (MBR) = number of longitudinal scale rows around body counted midway between axilla and groin; paravertebral scales (DSR) = number of scales in a paravertebral row from first scale posterior to parietal scale to last scale anterior to level of vent opening; fourth finger (4FS) and toe scales (4TS) = number of dorsal scales on fourth digit of hand and foot, distal scale contains claw, basal scale of fourth finger and toe lies adjacent to basal scale of third finger and toe respectively; fourth finger (4FL) and toe lamellae (4TL) - number of ventral scales on fourth digit of hand and foot, distal scale contains claw and basal scale is last largely undivided scale at a point level with intersection of third and fourth digits. Bilaterally scoreable scalation characters were scored on both sides and the mean value used in calculating statistics.

OSTEOLOGY. Specimens were X-rayed to assess phalangeal formula, and number of presacral and postsacral vertebrae.

Saproscincus oriarus sp. nov.

ETYMOLOGY. Latin *oriarus*, of the coast.

MATERIAL. HOLOTYPE: AMSR146851 Byron Bay, 3.5km N town centre (Byron Bay Holiday villages), NSW 28°37'S 153°35'E collected R. Sadlier & P. Rowland 11/2/1995. **PARATYPES:** AMSR146722, 146827 and 146747, all same general location and collectors as holotype (146722 site 5 3/2/1995; 146827, site 11 8/2/1995; 146747 site 3 6/2/1995); AMSR146634 Yuraygir NP, Blue Lake S Station Ck



FIG. 1. *Saproscincus orarius* from Byron Bay.

(area 89) NSW 29°57'S 153°14'E, 20/10/1994; AMSR144592 Yuraygir NP, N Wooli (NRAC 80 CG) NSW 29°49'S 153°16'E, 21/5/1994; AMSR150565 Coffs Harbour, Boultonwood St NSW 30°17'S 153°07'E, 25/11/1996; AMSR150941 Sawtell, Balydon NSW 30°21'S 153°04'E collected 4/4/1997; R132477 Limeburners Creek Nature Reserve, Big Hill rest/camping area NSW 31°16'S 152°58'E, 23/4/1989; AMSR146999 Myall Lakes area, Smiths Lake Field Station (vicinity) NSW 32°23'S 152°29'E.

DIAGNOSIS. The species described here is placed in the genus *Saproscincus* as defined by Greer (1989) in having six upper labials and a white spot to the posterior base of the thigh.

Saproscincus orarius is distinguished from the other members of the genus by the following combination of characters: adult size moderately small 34-43mm; premaxillary teeth 11; post-sacral vertebrae 54; nuchal scales meet behind interparietal; supraciliaries usually 6; scales on top of fourth finger 9-11; lamellae beneath fourth finger 13-16; scales on top of fourth toe 11-13; lamellae beneath fourth toe 18-22; lateral surface of head and body with a fine white midlateral stripe; dark markings on the ventral surface (when present) arranged in regular longitudinal rows.

DESCRIPTION. Based on 9 adults 34-43mm SVL (the single juvenile AMSR146722 is not

included in the description of scalation or measurements, and AMSR146634 is used only in scalation description due to poor preservation).

Measurements. (Adults only) Maximum SVL 43mm; distance from axilla to groin 53.7-57.9% SVL (mean = 55.6%, $n = 7$); distance from forelimb to snout 38.4-41.5% SVL (mean = 40.0%, $n = 7$); hindlimb length 34.2-39.0% SVL (mean = 36.9%, $n = 6$); tail approximately 1.5 $\times$ longer than body.

Scalation. Frontonasal broader than long; prefrontals moderately separated; frontal longer than wide, contacting first and second of four supraoculars; frontoparietals distinct; interparietal distinct, parietal eye spot present; parietals contact behind interparietal, each bordered by a nuchal scale and upper secondary temporal scale; primary temporal single; upper secondary temporal single, overlaps lower secondary temporal; lower secondary temporal single; tertiary temporal single; postlabials two.

Nasals moderately large, widely separated; loreals two; upper and lower preocular present; anterior suboculars one; supraciliaries usually six (75%), occasionally seven; upper labials six, fourth contacting the lower eyelid; lower labials six; postmental contacting first and second lower labial; chinshields three, first pair in broad con-

TABLE 1. Comparative table of measurements and meristics for *S. orarius*, *S. challengerii*, *S. rosei*, *S. spectabilis* and *S. mustelinus*. Data for *S. challengerii*, *S. rosei*, *S. spectabilis* from Sadler et. al., 1993.

	<i>S. orarius</i>	<i>S. challengerii</i>	<i>S. rosei</i>	<i>S. spectabilis</i>	<i>S. mustelinus</i> southern	<i>S. mustelinus</i> northern
Maximum SVL	43	57	64	59	58	55
TL (%SVL) range		137-168	137-192	139-192	175-202	152-191
mean	ca. 150	155.8	168.1	165.0	184.5	172.6
n	1	27	31	28	3	4
Sup. range	6-7	6-7	5-8	6-8	6-7	6-7
mode	6	6	7	7	6	6
MBR range	22-24	23-26	22-26	22-28	22-24	22-24
mean±sd	22.7±1.00	24.6±1.0	24.1±0.9	22.7±0.9	22.8±0.98	22.7±0.9
n	6	63	100	59	19	44
DSR range	59-63	54-63	55-67	54-61	56-62	58-65
mean±sd	61.0±1.32	57.6±1.6	58.8±2.2	57.9±1.7	59.8±1.45	61.0±1.67
n	6		101	58	19	44
4FS range	9-11	9-11	9-11	9-11	9-11	7-10
mean±sd	9.9±0.82	10.0±0.3	9.7±0.8	10.2±0.4	8.7±0.53	8.1±0.40
n	6	63	100	57	19	44
4FL range	13-16	15-19	14-18	16-21	10-14	9-12
mean±sd	14.2±0.80	17.3±0.9	15.3±0.9	17.9±1.0	12.7±0.73	10.9±0.68
n	6	63	100	57	19	44
4TS range	11-13	11-13	10-14	10-14	11-12	9-12
mean±sd	12.0±0.65	11.2±0.4	11.2±0.6	12.3±0.9	11.2±0.34	10.7±0.52
n	6	63	100	58	16	44
4TL range	18-22	22-27	17-24	22-28	18-22	14-19
mean±sd	19.9±1.1	24.3±1.0	21.0±1.2	24.8±1.4	19.8±0.62	16.8±1.14
n	6	63	100	63	19	44
Presacral range	28-29	27-29	27-29	26-28	28-30	29-30
mean±sd	28.3±0.52	27.1±0.3	27.7±0.7	27.0±0.3	29.1±0.43	29.3±0.48
n	6	16	58	46	17	42
Postsacral range	54	45-48	46-53	48-53	50-52	45-51
mean±sd		46.8±1.1	49.6±2.3	50.3±1.2	51.0±1.0	48.0±2.58
n	1	12	20	31	3	4

tact; lower eyelid with an obvious, centrally located semi-transparent disc; ear opening moderately large, with small acute lobules anteriorly and a number of small rounded lobules on posterior and lower edges.

Midbody scale rows 22-24 (mean = 22.7, sd = 1.00, n = 9); paravertebral scales 59-63 (mean = 61.0, sd = 1.32, n = 9); scales on top of fourth finger 9-11 (mean = 9.9, sd = 0.82, n = 8); lamellae beneath fourth finger 13-16 (mean = 14.2, sd = 0.80, n = 8); scales on top of fourth toe 11-13 (mean = 12.0, sd = 0.65, n = 8); lamellae beneath fourth toe 18-22 (mean = 19.9, sd = 1.10, n = 8).

Osteology. Presacral vertebrae 28 (n = 4) - 29 (n = 2); postsacral vertebrae 54 (n = 1); phalangeal

formula for manus and pes 2.3.4.5.3 and 2.3.4.5.4 respectively.

Colour and Pattern. Holotype and three paratypes from Byron Bay with mid brown dorsal surface, unmarked except for dark longitudinal streaks on scale row three (dorsolateral margin) before and after the fore- and hindlimbs. Lateral surface with a pale, dark-edged, mid lateral stripe (broken posteriorly) from behind nare to base of the hind limb, running under the eye, through the ear opening, and above the forelimb; upper lateral surface of body mid-brown, similar to dorsal colour; lower lateral surface mid to light brown approaching the venter. Fore- and hindlimbs with dark median streaks to each scale giving the ap-



FIG. 2. Records of *Saproscincus oriarus* (closed square) in NSW.

pearance of alternate light and dark brown stripes; anteriormost pale stripe of the hindlimb more or less continuous with pale mid lateral stripe. Tail markedly two-toned, dorsal surface lighter in colour than adjoining dorsal surface of body, lateral surface of tail same as body but with a prominent, pale, dark-edged stripe bordering the margin of the lateral and ventral surfaces. Ventral surface pale; scales of ventrolateral edge with a brown median streak forming a near continuous stripe down the body between the fore- and hindlimbs; underside of hindlimbs and enlarged median scales of tail with similar dark streaks.

The remaining specimens from further S show some variation with regard to intensity of colour, definition of the dorsal and lateral surfaces of the body, and degree of dark marking on the ventral surface of the body.

Two specimens (AMSR146634 & 144592) from two different locations at Yuraygir NP exhibit the extremes of variation in intensity of coloration. AMSR146634 is pale brown on the dorsal and lateral surfaces of the body but has a distinct

narrow, black, dorsolateral stripe on scale row 3, and the ventral surface nearly devoid of dark markings. AMSR144592 is dark brown on the dorsal surface and nearly black on the upper lateral surface of the body, and ventral scales of the body all have a dark median streak to giving the appearance of several parallel rows of dark stripes.

Two specimens from Coffs Harbour (AMSR-150565 & 150941), and one from Smiths Lake (146999), have well defined dark lateral and lighter dorsal surfaces, and moderate to extensive dark markings to the ventral surface (similar to 144592). The specimen from Crescent Head is similar in pattern but overall lighter in tone, and has less extensive dark markings on the ventral surface (similar to the Byron Bay specimens).

HABITAT AND DISTRIBUTION. Known from Byron Bay in the far NE of NSW to the Smiths Lakes area approximately 420km south. Habitat notes indicate the species prefers well vegetated areas along the central and northern coastal plain. The series of four specimens pitfall trapped on the coastal plain just N of Byron Bay represent 3 different habitat types: swamp sclerophyll forest dominated by broad-leaved paperbark, shrubs and ferns; swamp sclerophyll woodland/shrubland; and grassland that replaced native vegetation following clearing. The specimen from Limeburners Ck Nature Reserve was collected in an area that was, and is now adjacent to, littoral rainforest and *Melaleuca* swamp and the specimen from Smiths Lake field station was from coastal forest.

Data associated with several specimens indicate the species occurs in disturbed habitats. One specimen from Byron Bay was collected in an extensive area of mown grass, the specimen from Coffs Harbour from a suburban allotment, and the specimen from Limeburners Ck Nature Reserve 'in a pair of female underpants in tent habitat' located on grassland that was formerly littoral rainforest and *Melaleuca* swamp (H. Hines field notes).

Saproscincus oriarus appears to be a secretive species. All specimens collected from Byron Bay were taken from pit-fall traps between late afternoon and early morning.

One specimen collected in Oct. 1994 has 3 shelled eggs.

COMPARISON WITH OTHER SPECIES. Within *Saproscincus* Greer (1989) defined a lineage of three species *S. basiliscus*, *S. czechurae* and *S. tetradactyla*, all of which occur in closed forest habitat of mideast and NE QLD. This group of

species share the derived character states of small size, elevated number of premaxillary teeth (13 or more vs 11), and a unique arrangement of the nuchal scales. The second and third characters will readily distinguish these species from *S. oriarus*. A further two species similar to *S. basiliscus* have been described (Couper & Keim, 1998 [this volume]). Both are members of this lineage.

The remaining species *S. challengerii*, *S. rosei*, *S. spectabilis*, *S. mustelinus* and *S. oriarus* form a primitive assemblage within *Saproscincus*. *S. challengerii*, *S. rosei* and *S. spectabilis* are all moderately large diurnal species occurring in closed forest habitat of the coast and ranges of central and northern NSW and SE Qld. *S. mustelinus* is a crepuscular species that generally occurs in woodland rather than closed forest habitat. It is widely distributed in near coastal and highland areas of SE Australia but is only found in the highlands N of the Hunter R. in NSW. It is suggested these northern *S. mustelinus* are distinct from allopatric populations to the south (Wells & Wellington, 1985). *S. oriarus* also appears to be crepuscular in habits, but occurs in coastal or near coastal habitats N of the Hunter Valley and as such, is allopatric in distribution to both northern and southern populations of *S. mustelinus*.

In morphology *S. oriarus* can be distinguished from these remaining members of the genus as follows:

1) from *S. challengerii* in having fewer lamellae beneath the fourth finger (13-16 vs 15-19) and fourth toe (18-22 vs 22-27) and in having the dark markings on the ventral surface (when present) in regular longitudinal rows vs scattered;

2) from *S. spectabilis* by having fewer supraciliaries (usually 6 vs usually 7), and fewer lamellae beneath the fourth finger (13-16 vs 16-21) and fourth toe (18-22 vs 22-28);

3) from *S. rosei* in having fewer supraciliaries (usually 6 vs usually 7), and from southern populations of *S. rosei* in also having the dark markings on the ventral surface (where present) arranged in regular longitudinal rows vs scattered.

4) from the southern populations of *S. mustelinus* in having more finger scales (9-11 vs 8-10), more finger lamellae (13-16 vs 10-14), and presence of a fine midlateral stripe;

5) from northern populations of *S. mustelinus* in having more finger scales (9-11 vs 7-9), more finger lamellae (13-16 vs 9-13), more toe scales (11-13 vs 9-12), more toe lamellae (18-22 vs 14-20); and presence of a fine midlateral stripe.

Some female *S. challengerii* (Sadlier, 1993), *S. rosei* (Sadlier, 1993: figs 16, 18 & 19), and *S. spectabilis* (Sadlier, 1993: fig. 11) have a white midlateral stripe and two-toned body colour. Juvenile and subadult females of these species with a white midlateral stripe could be confused with similar sized *S. oriarus*. *S. oriarus* and *S. rosei* are regionally sympatric in the Coffs Harbour area on the mid north coast.

ADDITIONAL MATERIAL. *S. mustelinus* southern group: AMSR148294-299 Mt Wilson area, Waterfall Rd., 33°29'S 150°25'E NSW; AMSR148300 Mt Wilson, Waterfall Ck area, 33°30'S 150°23'E NSW; AMSR135309-310, 138135-146 Charlestown, Newcastle suburb 32°58'S 151°41'E NSW. *S. mustelinus* northern group: AMSR147088-91 Stewart's Brook SF, Gologlie picnic area 31°55'S 151°20'E NSW; AMSR148227-230 Riamukka SF, Hell Hole rd. near track to Grundy Fire Tower 31°20'S 151°39'E NSW; R148231-257 Riamukka SF, nr Grundy Fire Tower 31°20'S 151°39'E NSW; AMSR138212-215, 138232-242 Beech Lookout, Styx R. SF 30°31'S 152°21'E NSW.

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THE TAXONOMIC STATUS OF THE ECTOSYMBIOTIC FLATWORM *DIDYMORCHIS*, *PARANEPHROPIS* HASWELL

KIM B. SEWELL AND LESTER R.G. CANNON

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Didymorchis paranephraxis Haswell, 1900 which inhabits the branchial chamber of freshwater crayfish from New Zealand is the type species of the genus: its taxonomic status with relation to the Temnocephalida has been uncertain. We show it to have a multisyncytial epidermis and thus to belong in the Temnocephalida. The pattern of the mosaic of epidermal syncytia in this species differs slightly from those found in Australian species assigned to the genus. The Australian and New Zealand species currently assigned to *Didymorchis* are clearly members of the Temnocephalida, and they belong rightfully in their own family Didymorchidae Bresslau & Reisinger, 1933. The Australian species show several differences from the type species, especially in the form of the sclerotised male copulatory organ. The biogeography of the Didymorchidae suggests a Gondwanan lineage that predates the isolation of New Zealand in the upper Cretaceous (ca. 80mya) consistent with the idea that they are a group derived early in the evolution of the Temnocephalida. □ *Temnocephalida*, *Didymorchidae*, *crayfish*, *ectosymbionts*.

Kim B. Sewell & Lester R.G. Cannon, Queensland Museum, P.O. Box 3300, South Brisbane 4101, Australia; 1 December 1997.

Didymorchis paranephraxis Haswell, 1900 was described as a small ectosymbiotic worm which inhabits the branchial chamber of the New Zealand (NZ) parastacid crayfish *Paranephraxis zealandicus* (White, 1847). Haswell (1900) considered it a rhabdocoel turbellarian in the family Dalyelliidae, though he remarked on its resemblance to temnocephalans. Two further species (*D. cherapsis* Haswell, 1915 and *D. astacopsidis* Haswell, 1915) were described from Australian crayfish hosts. Haswell (1915) noted some differences, for example, in the excretory system and sclerotised male copulatory organ, and assigned the Australian species to the genus with some reservation. *Didymorchis* has been considered either a dalyelliid (Haswell, 1915; von Graff, 1904-1908; Baer, 1953, 1961; Karling, 1957; Williams, 1981; Cannon, 1986; Rohde & Watson, 1990a, b) or a temnocephalan (see Bresslau & Reisinger, 1933; Fernando, 1934; Fyfe, 1942; Hyman, 1951; Schaefer, 1971; Joffe, 1981, 1988; Joffe et al., 1995a; Rohde, 1994; Watson & Rohde, 1995a, b). Bresslau & Reisinger (1933) even proposed its own family, Didymorchidae, which several authors have accepted.

Bresslau & Reisinger (1933) believed *Didymorchis* was transitional between Temnocephalida and 'Dalyellioida' while Fernando (1934) considered them intermediate between the 'primitive' Scutariellidae and the more 'advanced' Temnocephalidae. Based on the distribu-

tion of temnocephalans and of their hosts, Schaefer (1971) supported the temnocephalan affinity of the Didymorchidae. His view was that *Didymorchis* was a primitive temnocephalan from which the Temnocephalidae, Scutariellidae and Actinodactylellidae were derived. Joffe (1981) and Joffe et al. (1995a) suggested that *Didymorchis* was derived early in the evolution of the Temnocephalida.

Why has there been uncertainty about the position of *Didymorchis*? The worms normally glide on cilia just as do most rhabdocoels, but Haswell (1900) claimed they showed evidence of looping, a character Williams (1981) postulated characteristic of temnocephalans. Temnocephalans have anterior tentacles according to Williams (1981) and *Didymorchis* lacks tentacles. More significantly, the sclerotised male copulatory organ of the type species figured by Haswell (1900) is very like that of dalyelliids, whereas that of Australian and South American species assigned currently to the genus are like that of a typical temnocephalan cirrus (see Haswell, 1915; Baer, 1953, 1961; Karling, 1957; Joffe, 1981, 1982). Baer (1953, 1961), who placed *Didymorchis* in the Dalyelliidae, suggested the male copulatory organ of *D. paranephraxis* is typical of simple dalyelliids. According to Karling (1957), however, it is closer to the strongly modified male copulatory organ of the dalyelliid *Hammalo-vortex nigrifrons* (Karling, 1934), though, as with

temnocephalans, it could be derived from that of *Alexlutheria*, the presumed primitive basal form of the dalyelliids. A South American species, *D. haswelli* Mañé-Garzon, 1960, and a variety, *D. haswelli* var. *australis* Dioni, 1972, have been described more recently with cirri close to those of Australian *Didymorchis* and thus typical of temnocephalans.

No new species of *Didymorchis* have been described since 1972, but ultrastructural studies of undetermined species of *Didymorchis* from Australian crayfish have provided support for the temnocephalan affinities of the Australian worms (see Rohde, 1987a, b; Rohde & Watson, 1990a, b; Watson & Rohde, 1995a, b). That the Australian species are temnocephalans was resolved by Joffe et al. (1995a) who determined that *D. cherapsis* and 3 undescribed species of *Didymorchis* from Australia had a 'multisyncytial epidermis', a characteristic of temnocephalans. The epidermis of temnocephalans is unique for the Platyhelminthes. It is syncytial (multinucleate fields arising through fusing of original cells) but comprised of several plates (Williams, 1986; Joffe et al., 1995a, b; Tyler & Tyler, 1997; Joffe & Cannon, 1998a). Some turbellarians have a syncytial epidermis but in the Neodermata, the whole body is, by contrast, covered by a single syncytium unbroken by cell membranes (Ehlers, 1985; Rieger et al., 1991; Joffe et al., 1995a; Tyler & Tyler, 1997; Joffe & Cannon, 1998a). *Udonella* is the only member of the Neodermata known with a separate syncytial field around its posterior sucker which is distinct from the remainder of its syncytial epidermis (Rohde & Watson, 1995; Tyler & Tyler, 1997). Joffe & Cannon (1998a) asserted that all described dalyelliids and dalyellioids have a cellular rather than syncytial epidermis. This is overwhelming evidence that the character 'syncytial epidermis composed of several syncytia' is a valid synapomorphy (a shared derived character) to distinguish the Temnocephalida from the family Dalyelliidae and/or suborder 'Dalyellioida'. Many of the characters used to historically discriminate temnocephalans from dalyelliids and other turbellarians are now known to be wrong or they are disputed.

The question of whether *Didymorchis* is temnocephalan nevertheless remains unanswered because the type species, *D. paranephropis*, from NZ has not been examined since Haswell (1900). Simply, does *D. paranephropis* from NZ have the syncytial mosaic typical of temnocephalans including the Australian species currently assigned to the genus, and concomitantly is the *Didymor-*

chidae a temnocephalan taxon? We aimed to solve these questions by examination of the epidermal topography of *D. paranephropis* and an analysis of characters used historically to define this controversial taxon.

MATERIALS AND METHODS

Six specimens of the crayfish *Paranephrops zealandicus* were collected at Powder Ck., Otago, NZ (45°61'S; 170°25'E) in April 1995 by Tim Dodgson (Department of Zoology, University of Otago, NZ), fixed in hot (ca. 60-90°C) 10% phosphate buffered formalin (HF) then transferred to 70% ethanol (etoh) and freighted to Brisbane. These provided fixed material of the worms. In March 1997, live worms were examined by LRGC in Dunedin from crayfish collected from the Taieri R., at 097867 on map 1-J44 'Dunedin' of the NZ Map Service in the second week of December 1996 by Ushio Nishitawa (Department of Zoology, University of Otago, NZ).

Live worms were observed using a stereo-microscope with transmitted and/or incident illumination. Worms were killed and fixed by flooding with a solution of 2% silver nitrate heated to ca. 60°C, washed in distilled water then exposed to bright sunlight or light from a cold light source for about 15-30 min. and either dehydrated down to 70% etoh and mounted in polyvinyl acetate (PVA) or dehydrated to 100% etoh and mounted in Euparal (Romeis, 1968; Joffe et al., 1995a, b).

Worms for wholemounts (WM) and scanning electron microscopy (SEM) were obtained from the host fixed in HF (see above). Hot fixation more clearly reveals the borders between the syncytia of the epidermal mosaic for SEM than does either ambient or cold fixation (Sewell & Cannon, 1995). Worms fixed for WM were rinsed in distilled water, stained with either Mayer's Haematoxylin (after Humason, 1972) (Hx), dehydrated in etoh, cleared in xylene and mounted in Canada balsam. Worms fixed for SEM, were rinsed 6 times in distilled water, dehydrated for 10 min in each of a graded series of ethanol, critical point dried, mounted on stubs and examined with a Hitachi S-530 SEM operating at 25kV. A Robinson backscatter detector was used to reduce charging. For examination of the sclerotic male copulatory organ, worms were placed in de Faure's medium (deF) either alive or after fixation in HF and rinsing in distilled water (Cannon & Sewell, 1995).

Photographs for figures were scanned from 35mm slides and negative film onto Kodak PhotoCD™, edited and assembled into plates using

Adobe Photoshop™. Lineart illustrations for figures were prepared by pen and ink, scanned using a Hewlett Packard flatbed scanner, edited and assembled into figures using Adobe Illustrator™.

TERMINOLOGY AND MEASUREMENTS. Terminology follows the conventions established by Cannon & Sewell (1995) and updated by Sewell & Cannon (1998). Specimens are deposited in the QM and slides are designated as either wholemounts (WM), de Faure's cirrus preparations (CP) or silver nitrate preparation (SN). The registered material examined is listed in the order: QM registration number, specimen/slide preparation details followed by only those data which are different from that of the preceding registration. For clarity, discrete blocks of registrations are separated by semi-colons.

Plasticity of shape and further distortion caused by the effects of fixative indicate that measurements are valuable only as a guide to the approximate size and shape of the worms and their internal structures. All measurements were made with the aid of a drawing tube. A range followed usually by the mean in parentheses is provided for each measurement; estimates are qualified and are preceded by ca. Where no range is provided the measurements were the same for all worms. Measurements are in μm unless otherwise stated. Descriptions of epidermal topography follow the terminology established for Australian *Didymorhis* spp. (see Joffe et al., 1995a).

DIDYMORCHIDAE

Bresslau & Reisinger, 1933

Didymorchis Haswell, 1900

TYPE SPECIES. *Didymorchis paranephraxis* Haswell, 1900.

OTHER SPECIES. *D. astacopsidis* Haswell, 1915. *D. cherapsis* Haswell, 1915.

SPECIES INQUIRENDAE. *D. haswelli* Mañé-Garzon, 1960. *D. haswelli* var. *australis* Dioni, 1972.

Didymorchis paranephraxis Haswell, 1900 (Figs 1A, 2-3)

MATERIAL. QMGL18670-18672, GL18674 (WM) ex branchial chamber *Paranephraxis zealandicus* from Powder Ck., Otago, NZ 45°61'S; 170°25'E April 1995 (Dodgson, T./Sewell, K.B. HF/Hx; GL18673 (CP[3], 3 adult specimens (1 damaged)) HF/deF; GL18677 (SN[5]) from Taieri R., Otago, NZ March 1997 (Nishitawa, U./Cannon, L.R.G.; GL18676 (CP[2], 2 adult specimens) deF; plus observation of living worms.

DESCRIPTION. *D. paranephraxis* was described by Haswell (1900) and is revised here. Small

dorsoventrally compressed worms to ca. 1mm long and less than 300 μm wide which inhabit the branchial chamber of their host and move by slow ciliary gliding. With posterior adhesive regions supplied with duct openings of rhabdite-forming glands. Pharynx cylinder-shaped and 'doliiform', ca $\frac{1}{6}$ th of the length of the body. Pigment absent except for that contained in a pair of eyes positioned posterior to pharynx. Body ciliated on the ventral surface but cilia absent from the lateral margins and dorsal surface. Excretory system with pores opening on the exterior on each side of ventral surface near the lateral margin. Male reproductive system composed of 2 somewhat oval-shaped testes situated close to the posterior border of the body; a copulatory bulb, sclerotised male copulatory organ with a tubular or rather funnel-like basal portion, and a distal portion composed of a number of spines; the basal portion is very wide at the proximal end, the greatest width being nearly equal to the length; spines are 10 or 12 in number; some straight and dagger-shaped, others curved and tapering. Female reproductive system with a single ovary, oviduct and uterus, paired vitelline glands, vitelline ducts and a vesicula resorbens but lacking a copulatory bursa.

The following measurements are provided to supplement Haswell's data. (Measurements based on 3 wholemount specimens QMGL18670-18671, GL18674 and 2 undamaged cirrus preparations GL18673).

External. Body from posterior margin to tip of anterior lobe 355-500 (413), to eyes 281-403 (334) long and 130-147 (136) wide.

General Anatomy. Pharynx 64-114 (89) long, 45-67 (57) wide. Eyes crescent-shaped ca 12 long, 5 wide and 33-42 (37) apart.

Reproductive System. Female. Ovary 20-28 (25) long, 16-19 (18) wide. Vesicula resorbens 23-33 (27) long, 17-27 (21) wide.

Male. Testes 73-106 (86) long, 28-48 (40) wide. Copulatory bulb 22-25 (23) long, 16-25 (20) wide. Male copulatory organ shaft cone-shaped, proximal opening 31-34 (33) wide, with narrow rim. Introvert (presumed) base angled, 21-23 (22) wide at base, lacks swelling and obvious distal opening. Spines large (all >15 long).

HOSTS. *Paranephraxis zealandicus* (White, 1847); Parastacidae.

LOCALITY. Otago Region, NZ.

REMARKS. Type specimens were not located in the collections of either the Otago Museum, Dunedin, NZ, or the Australian Museum, Sydney, or

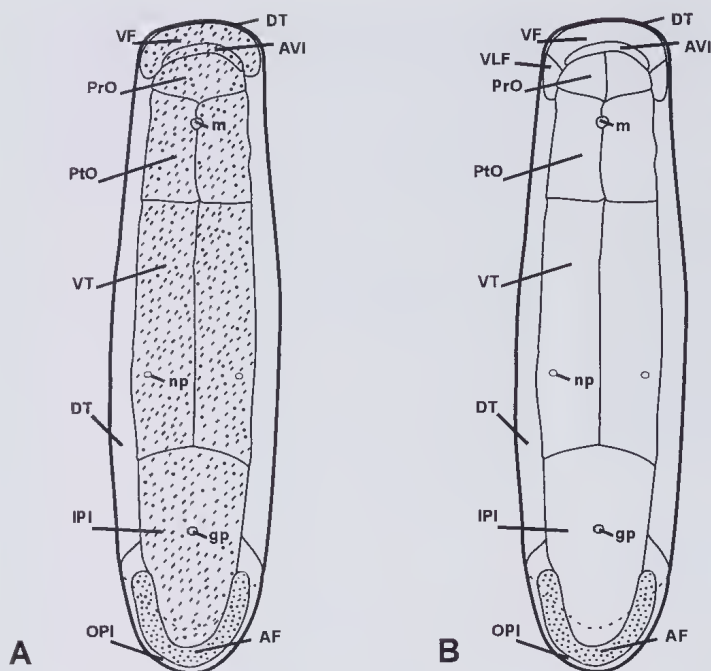


FIG. 1. A, mosaic of epidermal syncytia for *Didymorchis paranephropis* in ventral view. B, mosaic of epidermal syncytia suggested for the archetype of the Temnocephalida in ventral view. AF = adhesive field syncytium; AVI = anterior ventral intermediate syncytium; DT = dorsal trunk syncytium; gp = gonopore; IPI = inner posterior intermediate syncytium; m = mouth; np = nephridiopore; OPI = outer posterior intermediate syncytium; PrO = preoral syncytium; PtO = postoral syncytia; VLF = ventral lateral syncytia; VF = ventral frontal syncytium; VT = ventral trunk syncytia (terminology after Joffe et al., 1995a). Locomotory cilia are represented by fine oblique dashes.

the McLeay Museum, University of Sydney, Australia. Haswell, apparently failed to lodge type specimens. There is, however, no doubt that the worms redescribed here are specimens of *D. paranephropis* which remains the only species of the genus known from NZ.

Epidermis. Haswell (1900) noted that ciliation was confined to the ventral body and the epidermis is a 'thin protoplasmic layer with nuclei at wide intervals', but later (Haswell, 1915) he says of *Didymorchis* that the integument 'is entirely devoid both of cell-boundaries and of nuclei', inferring that both NZ and Australian representatives had a syncytial epidermis with insunk nuclei. Mañé-Garzon (1960) described and figured scarce, though well stained, intraepidermal nuclei of *Didymorchis haswelli* from South America, but also figured, without comment (see Mañé-Garzon, 1960 plate III, Fig. 1), structures which may be interpreted as cytoplasmic processes to insunk nuclei. Insunk nuclei are charac-

teristic of Australian *Didymorchis* (see Rohde & Watson, 1990a; Joffe et al., 1995a). Intraepidermal nuclei, however, have also been demonstrated in an unidentified Australian *Didymorchis* by Rohde & Watson (1990a) who found such nuclei rarely and always isolated from the epidermis by a membrane (see Rohde & Watson, 1990a [Fig. 17]).

Silver nitrate staining and SEM both revealed an epidermal mosaic (Figs 1A, 3). The epidermis of *D. paranephropis* has 11 syncytia (Fig. 1A) of which 2 are 'paired': dorsal trunk syncytium (DT), ventral frontal syncytium (VF), anterior ventral intermediate syncytium (AVI), preoral syncytium (PrO), postoral syncytia (PtO) (paired), ventral trunk syncytia (VT) (paired), inner posterior intermediate syncytium (IPI), outer posterior intermediate syncytium (OPI) and adhesive field syncytium (AF). These can be divided into 6 'groups': ciliated syncytia over the ventral side of the body except the frontal part (2 VTs, 2 PtOs and PrO); the main unciliated epidermal syncytium (DT); syncytia of the ventral anterior part of the body (VF); syncytium of the adhesive

field (AF); small syncytia that separate the adhesive field from the major epidermal syncytia (IPI & OPI); and the AVI. These 6 groups were found also in Australian species referred to *Didymorchis* by Joffe et al. (1995a) who related them to structure and function.

Comparison between the mosaic of *D. paranephropis* and the Australian species shows *D. paranephropis* has 11 syncytia of which 2 are 'paired' while the Australian species have 12-14 syncytia of which 2-3 are 'paired' [Joffe et al. (1995a) (Fig. 1A)]. There are other differences in the mosaic: 1, the VT of *D. paranephropis* is divided by a mid ventral suture, i.e. the VT is 'paired' sensu Joffe et al. (1995a), though the nephridiopores of all species are found in the VT; 2, no VLF are present in *D. paranephropis*; 3, the gonopore is located in the IPI of *D. paranephropis*, and within the VT of the Australian species; 4, the IPI of *D. paranephropis* is covered with dense locomotory cilia whereas ciliation is



FIG. 2. Cirrus of 2 adult specimens of *D. paranephraxis* QMGL18673 ex type host and locality. Note that the cirrus spines of the specimen on the right are spread more widely than those of the specimen on the left and are articulated at their proximal insertion. Scale = 100 μ m.

sparse in the Australian species; and 5, the OPI circumscribes the posterior region of the body of *D. paranephraxis* (Figs 1A, 3A-G) whereas in the Australian species, the entire OPI is on the ventral surface. Although only a small number of specimens was available for examination, intraspecific variability in the mosaic was observed; the junction of the paired VT and PtO was offset from the mid-line in several specimens (Fig. 3B).

Locomotion. *Didymorchis paranephraxis* moves only by ciliary gliding. The worm becomes elongate, with the anterior end and the posterior adhesive field carried above the substrate when gliding in a straight line. The anterior end regularly 'searches' the substrate but was never observed to attach the worms firmly during locomotion. *D. paranephraxis* alters course by gentle lateral movements of the body to achieve slight angle changes in direction. Large angle changes are accomplished by first attaching the posterior adhesive field, rotating the body about the attachment, releasing the attachment and then moving off in the new direction. *D. paranephraxis* invariably contracts the posterior of the body forward before placing the adhesive region, which is well supplied with rhabdites, down onto the substrate; this is particularly noticeable when worms, gliding linearly with the body elongated, encounter an obstacle in their path. The pad may be observed to flatten and widen at the exact moment of con-

tact with the substrate. Haswell (1900) claimed that *D. paranephraxis* were able to 'loop' using attachment of both the anterior lobe and posterior adhesive pad, but we did not observe the worms to move in this way. Specimens in a thin film of water between a glass slide and coverslip, however, were seen to progress forwards using 'peristaltic' movements of the body and internal organs, an action which superficially resembles looping but which does not include attachment of the anterior lobe to the substrate. This form of locomotion is therefore an artifact and simply is a response to restricted movement such as that caused by the pressure of a coverslip.

Male Copulatory Organ. The distinctive form of the sclerotised male copulatory organ was figured by Haswell (1900) (compare Haswell (1900 [Plate XXI, 3]) with Fig. 2). Unlike the cirrus of *Didymorchis cherapsis*, *D. astacopsidis*, *D. haswelli* and *D. haswelli* var. *australis*, it lacks an apparent introvert with an obvious introvert base and introvert swelling, characters 'typical' of temnocephalans. Eversion of the male organ could not be determined in the fixed material, nor was it observed to evert when seen alive, though such an event is not readily induced and its possibility cannot be ruled out. The shaft and proximal articulations of the spines of the copulatory organ were enclosed in a robust band of muscle. Individual spines were observed to move/articulate, though only a few degrees.

Excretory System. Haswell (1900) claimed the excretory system of *D. paranephraxis* opened on the ventral surface through two pores lateral to the posterior extremity of the pharynx, and that internal to the pores was a granular mass through which the duct coiled. Though clearly evident in even juveniles of small temnocephalans such as *Craspedella* spp., careful examination of live *D. paranephraxis* and all the available wholemounts failed to reveal any evidence of excretory ampullae in the NZ worms, so it is unclear to what 'granular mass' Haswell was referring. Later, in describing the excretory system of Australian representatives of *Didymorchis*, Haswell (1915) noted the excretory pores lacked any 'intercalation of any excretory sac or vesicle'. He said also the pores in the Australian species were more posterior, though we observed the tiny nephridiopores of *D. paranephraxis* are located, as in the Australian *Didymorchis*, about in the same relatively posterior position. Finally, Haswell (1915) said of the Australian species the arrangement of ducts 'differs completely from that which occurs in *D. paranephraxis*', though

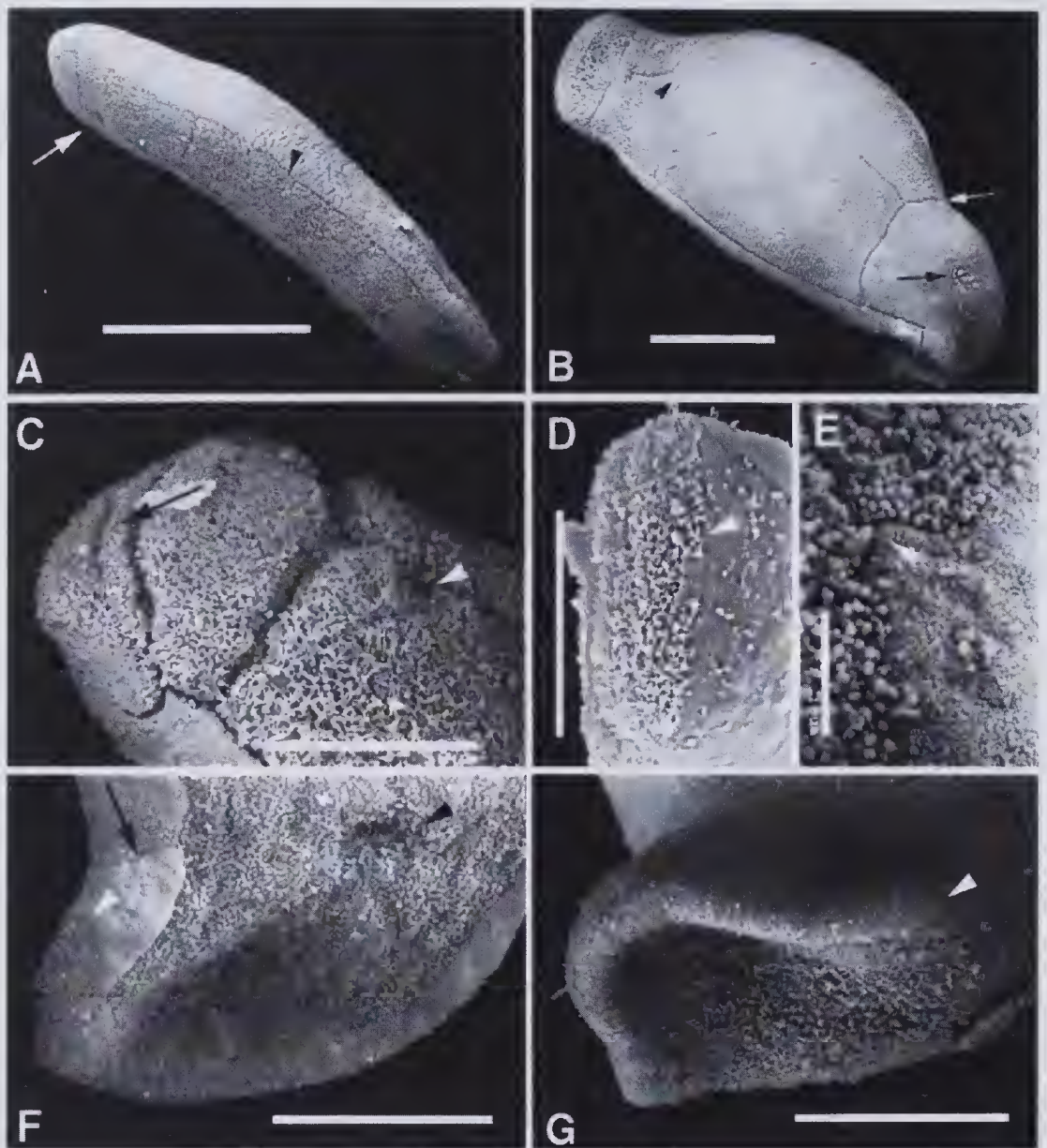


FIG. 3. SEM epidermal topography of *D. paranephraxis* fixed in HF. Terminology for the syncytia from Joffe et al. (1995a) and Fig. 1. A, ventrolateral view of whole specimen showing pattern of the epidermal mosaic and position of the mouth (arrow). Arrowhead indicates border between the DT and the VT. Scale = 200 μ m. B, ventral view of whole specimen with posterior end curled dorsally at a point just posterior to the border between the OPI and DT (white arrowhead) to show the border between the VT and IPI (white arrow) and position of the gonopore (arrow). Note the 'offset' junction of the paired VT and PTO (black arrowhead) typical of most individuals examined. Scale = 100 μ m. C, ventrolateral view of anterior end showing dense locomotory cilia and pattern of the epidermal mosaic with position of the AVI indicated by an arrow and the mouth by an arrowhead. Scale = 50 μ m. D, en face view of the anterior end showing the VF. The border of the VF and DT is indicated by an arrowhead. Scale = 50 μ m. E, lateral view of right side of the anterior end to show junction of the borders of the VF, AVI and DT (arrowhead). Scale = 10 μ m. F, ventral view of the poster end to show position of the gonopore (black arrowhead) and border between the OPI and DT (arrow) and border between the AF and the OPI (white arrowhead). Scale = 50 μ m. G, posterior end to show horse-shoe shaped AF and border between the AF and the OPI (arrowhead). Scale = 50 μ m.

his account seems insufficiently different to warrant such a strong statement.

DISCUSSION

The type species *D. paranephraxis* is temnocephalan because it has a multisyncytial epidermis (Joffe & Cannon, 1998a). Furthermore, the similarity of the epidermal mosaic with that of the Australian representatives of the genus attests to their close relationship and confirms Didymorchidae as a recognisable taxon. Although it is not yet confirmed for all temnocephalan genera, a multisyncytial body wall epidermis has been described for all temnocephalans examined for the character (see Nichols, 1975; Williams, 1975, 1979, 1981, 1982, 1986, 1991, 1992; Joffe & Dzhanchvili, 1981; Joffe, 1982, 1988; Joffe et al., 1995a, b; Sewell & Cannon, 1995, in press; Sewell, 1998; Joffe & Cannon, 1998a). Joffe et al. (1995a) and Joffe & Cannon (1998a) suggested that the total number of syncytia has been reduced in the evolution of temnocephalans, i.e. the apomorphic (derived or advanced) state has fewer syncytia. *D. paranephraxis* with 11 syncytia, shows more apomorphic characters than the 4 Australian species in the genus with 12–14 syncytia (Joffe et al., 1995a). The relative importance in the mosaic of 'paired' or isolated neighbouring syncytia with the same structure and 'groups' of syncytia correlated by their functional specialisations should, however, be considered in any attempt to elucidate the evolution of the epidermal mosaic (Joffe & Cannon, 1998a). In any case, the differences in the mosaic between the Australian and NZ species and the interspecific and intraspecific variation between Australian *Didymorchis* observed by Joffe et al. (1995a), support the hypothesis of Joffe & Cannon (1998a) that the ancestral form had more syncytia than are retained by the extant species. Joffe & Cannon (1998a) suggested that the mosaics of the Scutariellidae and the Didymorchidae arose independently from a primitive stage characterised by a higher number of syncytia covering the trunk and a horseshoe-shaped AF syncytium. We propose an archetypal mosaic for the Temnocephalida (Fig. 1B) based on the total number of syncytia now recorded for species of *Didymorchis* (this study; Joffe et al., 1995a; Joffe & Cannon, 1998a) and on the model of evolution of the epidermal mosaic proposed by Joffe & Cannon (1998a).

Presumably, the unique multisyncytial epidermis of temnocephalans has evolved as an adaptation to symbiosis in a freshwater environment,

however, many questions remain to be resolved about the phylogeny of the epidermis, particularly between turbellarians and the Neodermata (Tyler & Tyler, 1997; Joffe & Cannon, 1998a). It is paradoxical that the primitive temnocephalan, *Didymorchis*, has insunk nuclei similar to those in the Neodermata, whereas other, presumably more advanced, temnocephalans all have intraepidermal nuclei, a character believed generally to be more primitive (Rohde, 1987a; Joffe et al., 1995a; Tyler & Tyler, 1997).

There is mounting support for the argument that temnocephalans are 'dalyellids' that have become ectosymbiotic and developed new characters (Ehlers, 1985; Ehlers & Sopott-Ehlers, 1993; Rohde et al., 1993, 1995; Rohde, 1996; Joffe & Cannon, 1998b). The characters used historically to separate *D. paranephraxis* from temnocephalids are either wrong or at best debatable. Baer (1931) and Williams (1981) maintained a looping method of locomotion was the main characteristic that separated temnocephalans from other turbellarians. Furthermore, Williams (1986) stated that temnocephalans lacked locomotory cilia and had anterior tentacles. These characters are wrong, because *D. paranephraxis*, like the undisputed temnocephalan *Diceratocephala boschmai* Baer, 1953, do not loop and move only by locomotory cilia (Cannon, 1991; Jones & Lester, 1992; Joffe et al., 1995b). Fyfe (1942) was correct when she asserted that the absence of tentacles in *Didymorchis* was not sufficient reason to exclude it from the Temnocephalida.

The sclerotised male copulatory organ of *D. paranephraxis* differs from the cirrus figured for *D. cherapsis* and *D. astacopsidis* from Australia (Haswell, 1915, figs 6,7) and *D. haswelli* (see Mañé-Garzon, 1960, pl. 4, figs 1,2) and *D. haswelli* var *australis* (see Dioni, 1972, figs 7–11) from South America. The cirrus in the Australian and South American species is 'typical' of most temnocephalans with an introvert lined with rows of relatively short spines. By contrast, the male copulatory organ of *D. paranephraxis* has only a few extremely large and elongate spines which appear to be articulated individually by muscles and may not form a 'typical' introvert. Moreover, a large band of muscle surrounds the base and proximal spine articulation, and the organ apparently lacks an 'introvert swelling' (sensu Cannon & Sewell, 1995). The differences between the size and number of spines in the Australian and NZ species were noted by Haswell (1915). The arrangement of these large spines in *D. paranephraxis*

ropis certainly resembles the 'typical' male intromittent organ of the Dalyelliidae (Baer, 1953; Luther, 1955), however, recent studies on the Craspedellinae by Cannon & Sewell (1995) and Sewell & Cannon (1998) confirm that the shape and form of the temnocephalan cirrus is not a reliable character to discriminate genera. *Craspedella pedum* Cannon & Sewell, 1995 for example has a unique cirrus with a strongly-reflexed shaft and a permanently everted introvert composed of flat, plate-like teeth, whereas all other species of the Craspedellinae (in the genera *Craspedella*, *Heptacraspedella*, *Zygopella* and *Gelasinella*) have, by contrast, a typical temnocephalan cirrus (Cannon & Sewell, 1995; Sewell & Cannon, 1998). Thus, although the form of the cirrus in the Australian species assigned to *Didymorchis* is more typically temnocephalan than that of the type species of the genus, the differences in our opinion, considering the other similarities between the worms, do not warrant erection of a new genus for the Australian species.

The presence of an epidermal mosaic has not been confirmed for the South American species assigned to *Didymorchis* and thus their status as temnocephalans is not yet established firmly. The morphology of the reproductive structures in *D. haswelli* and *D. haswelli* var. *australis* from South America, particularly that of the cirrus, nevertheless suggests that they too are temnocephalan and probably closer to the Australian than to the NZ species. Nevertheless, until the temnocephalan status of the South American species is confirmed, the temnocephalan family Didymorchidae originally erected by Bresslau & Reisinger (1933) can accommodate with certainty only the Australian and NZ species assigned currently to *Didymorchis*.

We propose therefore the following family diagnosis:

DIDYMORCHIDAE
Bresslau & Reisinger, 1933

Temnocephalida with elongate cylindrical body, without lateral ridges and lacking tentacles. Epidermis composed of 11-14 epidermal syncytia. Pigment confined to a single pair of anterodorsal eyes. Posterior adhesive field (attachment organ) not pedunculate or circular and without a marginal valve. Dorsal surface without imbricating scales or raised body ridges. Locomotory cilia confined to the ventral surface. Buccal cavity or pre-pharynx conspicuous; pharynx large and directed anteroventrally. Gut without colour or septa. Eyes present, small, discrete and widely

spaced. Gonopore midventral in posterior third of body. Seminal receptacle single; vitellaria restricted to a pair of lateral cylinders. Testes, 1 pair posterior, spherical to ovoid, positioned posterior to gut. Small, slender worms ca 1mm in vivo. Inhabiting the branchial chamber of their freshwater crustacean hosts.

Didymorchidae occur on parastacid crayfish in Australia and NZ and have been described from South America, therefore, they have an 'amphinoctic' or 'circumantarctic' Gondwanan lineage (Banarescu, 1990). The ancient Gondwanan distribution of *Didymorchis* is consistent with the hypothesis that the Didymorchidae are an early derived group of Temnocephalida. In Australia the Didymorchidae are found on both *Cherax* and *Euastacus* crayfish and they have a widespread distribution. *Didymorchis* were described by Haswell (1915) from crayfish in eastern Australia and he mentioned an 'allied form' from a Tasmanian crayfish *Astacopsis australiensis* Haswell, 1882 [according to Clark (1936) this crayfish species is a secondary synonym of *Euastacus serratus* but as *Euastacus* does not occur in Tasmania (Hamr, 1992), the identity of this host remains uncertain]. The worms also occur on *Cherax* from Western Australia and the Northern Territory (unpublished observations). The absence of the Didymorchidae from India and Africa and their presence in NZ, suggests that they evolved after India, but before NZ separated from Gondwanaland (Heatwole, 1987). Alternately, the worms may never have existed in the African and Indian regions of Gondwanaland or they may have become extinct in these regions after the breakup of the southern supercontinent. We predict that the Australian and South American species of *Didymorchis* will be shown to differ less from each other than from the type species, *D. paranephropis*, because of the earlier separation of NZ from Gondwanaland.

Finally, the controversy about the taxonomic position of the ectosymbiont *Varsoviella kozminskii* Gieysztor & Wiszniewski, 1947 from the gills of gammarids from the Vistula R. in Poland is analogous to that for *D. paranephropis* before our study. Like *D. paranephropis*, *V. kozminskii* has been classified hesitantly as a dalyelliid, with attention drawn to its temnocephalan similarities (Gieysztor & Wiszniewski, 1947; Luther, 1955; Matjasic, 1990; Ehlers & Sopott Ehlers, 1993; Rohde, 1996). The sclerotised male copulatory organ of *V. kozminskii* is strikingly similar in general form to that of *D. paranephropis*. Like *D. paranephropis*, the male organ of *V. kozminskii*

has a few large dagger-shaped spines, and *V. kozminskii* has not been examined since it was first described. It may, therefore, be instructive to examine the epidermis of *V. kozminskii* to help resolve its taxonomic position. Matjasic (1990) proposed that, if a temnocephalan, *Varsoviella* could be placed in its own family Varsoviellidae.

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A NEW SEMI-SLUG FROM TAMBORINE MOUNTAIN, SOUTHEASTERN QUEENSLAND (MOLLUSCA: EUPULMONATA: HELICARIONIDAE)

JOHN STANISIC

Stanisic, J. 1998 06 29: A new semi-slug from Tamborine Mountain, southeastern Queensland (Mollusca: Eupulmonata: Helicarionidae). *Memoirs of the Queensland Museum* 42(2): 597-603. Brisbane. ISSN 0079-8835.

The helicarionid semi-slug, *Cucullarion parkini* gen. et sp. nov., is described from the rainforests of Tamborine Mountain, southeastern Queensland. Its relationships and isolation in these upland refugia are discussed in relation to climate-induced shifts in the distribution of wet rainforest in eastern Australia since the mid- to late Tertiary. □ *Mollusca, Eupulmonata, Helicarionidae, semi-slug, biogeography.*

John Stanisic, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 10 July 1997.

Helicarionid semi-slugs have diversified greatly in the humid rainforests of eastern Australia. These perennially moist environments are ideally suited to terrestrial molluscs which have a weakly to non-calcified, reduced shell into which the animal cannot fully withdraw. A comprehensive review of the group has yet to be completed and there are still many species to be described from the eastern Australian region. However, Kershaw (1979, 1981, 1983) and Stanisic (1993a, b) have advanced our knowledge of this group considerably. Several species are known from southeastern Queensland (SEQ) (Smith, 1992; Stanisic, 1995) but the taxonomic status of the majority of these has yet to be rigorously tested by detailed anatomical examination. This study describes a new species of semi-slug from Tamborine Mtn, SEQ which is characterised by extreme reduction of the shell and strong development of the shell lappets and mantle lobes.

STUDY AREA

Tamborine Mtn is located c. 80km SW of Brisbane (Fig. 5) and is part of a large basaltic plateau (Darlington Ra.) which is a northward extension of the MacPherson Ranges (MacDonald, 1988). Average annual rainfall is 1600mm and year-round humidity is high (MacDonald, 1988). Volcanically derived soils (red earths) support moist subtropical rainforest (as complex notophyll vine forests) on the mountain summit. At lower altitudes these evergreen rainforests (with large stands of the palm *Archontophoenix cunninghamiana*) are also able to survive in moist refuges such as gullies and along watercourses (Webb, 1988). Aboriginal man, and more recently Europeans, have greatly influenced contemporary vegetation patterns (Webb, 1988). Much of the

mountain was cleared in the early part of this century (Ross, 1988) and it is probably fortuitous that remnant patches of rainforest survive at all. Many of these remnants are in fire-proof niches such as the less accessible steeply sided gorges which occur on the mountain's extensive slopes.

SYSTEMATICS

The classification used in this study follows Smith (1992) unless otherwise stated. Anatomical abbreviations follow Solem (1966, 1976) and are explained in the text.

Order EUPULMONATA
Sub-order STYLOMMATOPHORA
Family HELICARIONIDAE

Cucullarion gen. nov.

ETYMOLOGY. Latin *cucullus*, cowl; referring to the hood-like appearance of the mantle lobes.

TYPE SPECIES. *Cucullarion parkini* sp. nov.

DIAGNOSIS. Shell degenerate, almost plate-like with incomplete internal whorls. Whorls relatively few with obsolete sculpture. Animal with strongly developed shell lappets and mantle lobes, long slender foot, dorsally keeled tail and prominent caudal horn. Genitalia with epiphallic flagellum but no epiphallic caecum. Penis internally with sculptured longitudinal pilasters, weak pustules and a subcylindrical verge with subterminal epiphallic pore.

COMPARISONS. *Cucullarion* gen. nov. differs most notably from the northeastern Queensland (NEQ) *Fastosarion* Iredale, 1933 by having a much smaller shell with incomplete internal whorls and in the male genitalia lacking an epiphallic caecum and having a penis with a verge (Scott, 1995). *Thularion* Stanisic, 1993 from NEQ

has a shell with incomplete internal whorls but which is much larger and strongly spirally sculptured. An epiphallic caecum is present and the penis is greatly elongated with pustulose sculpture internally, a prominent lamellate pilaster in the upper half and no penial verge. *Eungarion* Stanisc, 1993 from mideastern Queensland (MEQ) has a shell which is much smaller than that of *Cucullarion* but which is similarly reduced and lacking in spiral sculpture. An epiphallic caecum is present and the penis has internal sculpture of strongly rounded pustules, two prominent pustulose pilasters and an apical verge which opens terminally. *Parmacochlea* Smith, 1884 from far N Queensland has a small, flat plate-like shell without membranous margins, penis with strongly nodulose pustules internally and a verge with a terminal pore.

Helicarion sensu stricto from SE Australia has a shell with complete internal whorls. It lacks an epiphallic caecum, however more significantly, it possesses an epiphallic gland (Kershaw, 1981). This structure has yet to be recorded in any 'northern' semi-slug genera (Hedley, 1893; Scott, 1995; Stanisc, 1993a,b) and probably reflects a major phyletic division within the eastern Australian semi-slugs. These accessory epiphallic structures are probably concerned with spermatophore formation and most likely determine the shape of the sperm packet. Stanisc (1993b) has previously suggested that there are major differences in the form of spermatophores between southern and northern east-coast helicarionids which may transcend the level of species isolating mechanisms and indicate broader evolutionary relationships. Unfortunately the material studied did not contain spermatophores.

***Cucullarion parkini* sp. nov.**
(Figs 1-4)

ETYMOLOGY. For Roger Parkin who purchased the naming rights of the species at the Queensland Museum's tenth anniversary celebratory dinner.

MATERIAL. HOLOTYPE: QMMO60128, shell and preserved animal, The Knoll NP, Tamborine Mtn, SEQ, notophyll vine forest/palms, climbing palm trees after rain. Coll. J. Stanisc, D. & N. Potter, J. Chaseling, 26 Feb 1985. Major diameter of shell 14.94mm, minor diameter 9.09mm, height 3.25mm, H/D ratio 1.64, whorls 2 3/8; length of preserved animal 37.22mm. **PARATYPES:** QMMO20858, 9 preserved animals, 1 shell, same data as holotype; MO27502, 1 shell, Tamborine Mtn, SEQ, Colliver Collection.

DESCRIPTION. Shell (Fig. 1) of average size for family, glossy, lenticular, very thin, fragile and almost plate-like, maximum diameter 14.94-



FIG. 1. Shell of *Cucullarion parkini* sp. nov., holotype, QMMO60128. Upper, apical view. Lower, basal view. Scale in mm.

15.58mm (mean 15.26mm), minimum diameter 9.09-9.35mm (mean 9.22mm). Spire not elevated. Height of shell 1.95-3.25mm (mean 2.60mm), H/D ratio 1.64-1.67 (mean 1.66). Whorls 2 3/8-2 7/8 (mean 2 5/8), expanding rapidly, without internal walls. Body whorl expansive, weakly rounded toward the edges, margins membranous. Protoconch of 1 1/4 whorls, smooth. Post-nuclear sculpture of weak arcuate growth lines. Sutures margined, barely impressed. Colour yellow with few arcuate darker streaks; apex white. Based on 2 measured specimens (QMMO60128, MO27502).

Animal (Fig. 2) comparatively large, body length (in preservative) to 47.70mm (mean 44.74mm, n=3). Foot slender, tripartite, rounded anteriorly, weakly tapered posteriorly; tail relatively long, high, sharply keeled mid-dorsally; caudal horn and foss very prominent. Pedal grooves conspicuous, situated relatively low down on the sides of the foot. Colour (in life) beige with diffuse grey markings on visceral hump and sides of tail; antero-dorsal region of tail and edges of foot with light yellow markings; slime reticulation yellow on the tail, grey on neck and anterior sides of the foot; sole of foot off-white. Skin texture (in 70% ethanol) smooth; (in life) mainly smooth but with microscopic pustules on shell lappets and mantle lobes (Fig. 2C). Right mantle lobe (RML) small, narrowly elon-



FIG. 2. Live animal of *Cucullarion parkini* sp. nov., holotype, QMMO60128. A, side view. B, top view. C, close-up of visceral hump to show shell lappets and mantle lobes with minute pustulations.

gate, fused to right shell lappet (RL) posteriorly and with a short lobular extension anteriorly. Left mantle lobe (LML) a cowl-like extension over the neck region, fused to the left shell lappet posteriorly; shell lappets fused to each other both anteriorly and posteriorly. Shell barely visible (Fig. 2B).

Genitalia (Fig. 3A) with ovotestis (G) consisting of several lobes of cream coloured alveoli embedded in the apical whorls of the digestive gland. Hermaphroditic duct (GD) relatively long and convoluted. Talon pear-shaped with a short stalk. Carrefour not conspicuous. Albumen gland (GG) a mass of creamy-brown acini. Prostate-uterus compacted. Uterus (UT) conspicuously sacculate; prostate (DG) a narrow band of creamy-coloured alveoli appressed to the uterine surface for the entire length. Vas deferens (VD) long and strongly convoluted. Epiphallus (E) longer than penis, muscularised, bound to penial sheath by connective tissue, internally with several rows of longitudinally arranged, sub-rectangular pustules; inserting on penis apically. Epiphallic flagellum (EF) moderately long and arising at epiphallus-vas deferens junction, bound in connective tissue. Penial retractor muscle (PRM) inserting on epiphallus at about one third of its length from penis. Penis (P) cylindrical with a muscularised sheath (PS) for its entire length; internally (Fig. 3B) with a long central, sculptured, longitudinal pilaster (PPM), a short sculptured apical pilaster (PPS) and several narrower, sculptured longitudinal pilasters (PP). Otherwise with low, irregularly shaped, sometimes subcircular (particularly apically) but generally elongate pustules and low, very narrow, longitudinal thickenings basally. Epiphallic pore (EP, Fig. 3C) located laterally on a sculptured vergic papilla (PV). Free oviduct (UV) short, internally with broad transverse thickenings. Spermatheca (S) with an expanded stalk (SS) and clavate head appressed to the prostate-uterus about three quarters distance along its length from the free oviduct. Vagina (V) very short, internally with transversely arranged thickenings. Atrium (Y) very short.

Radula with a tricuspid central tooth (Fig. 4A) with a basal plate which has two prominent lateral support ridges and a well developed anterior flare (Fig. 4B, C); basically bicuspid lateral teeth with greatly reduced endocone located high up on mesocone (Fig. 4A); and a very large number of marginal teeth (Fig. 4D, E) that are bicuspid with long sinuate shafts which become denticulate along their outer edge in the outer marginals. Radular formula approximately 130.14.1.14.130. Jaw (Fig. 4F) strongly arcuate without prominent sculpture.

Based on 2 dissected specimens (QMMO20858, MO60128).

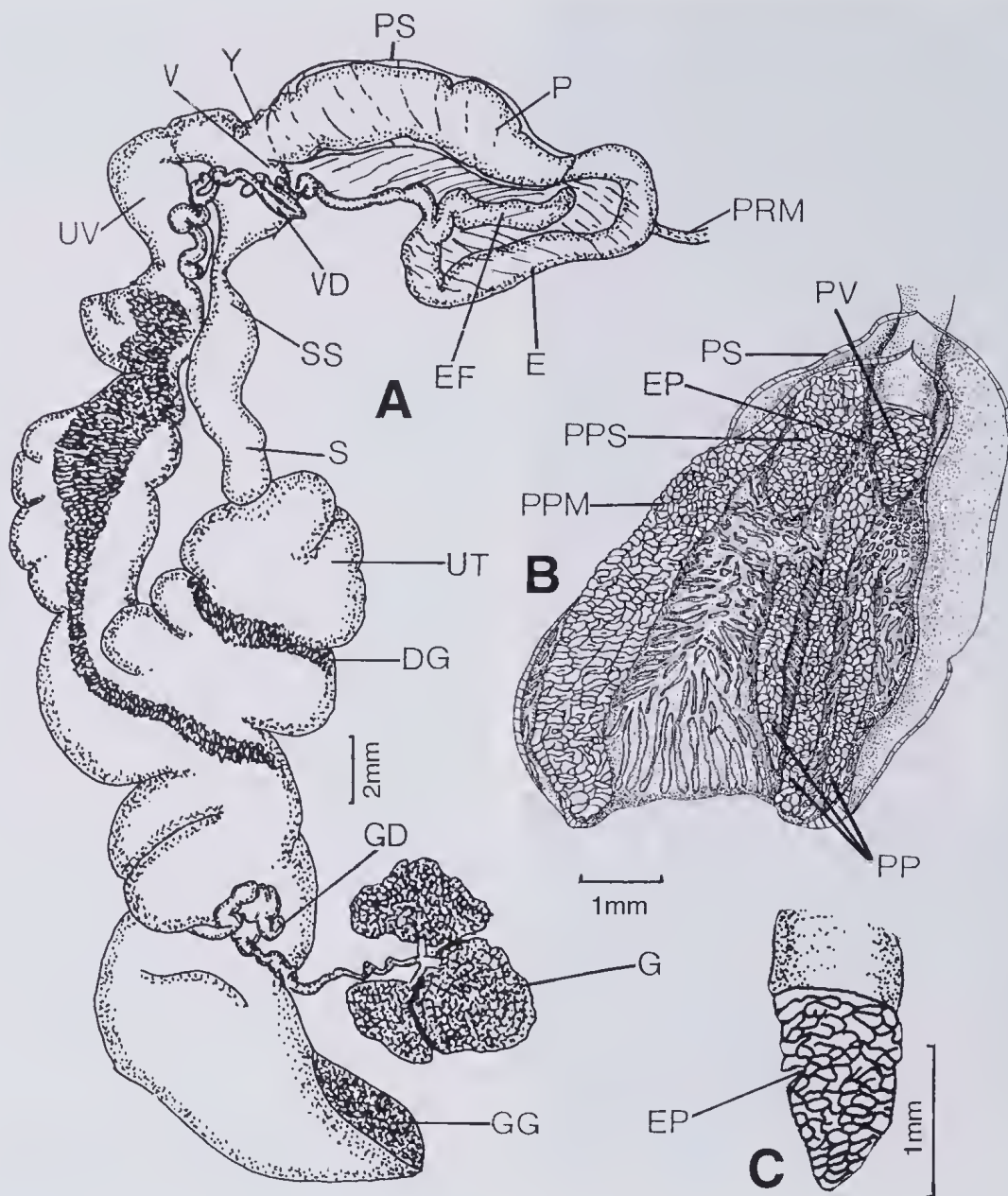


FIG. 3. *Cucullarion parkini* sp. nov., holotype, QMMO60128. A, reproductive system. B, penis interior. C, details of penial verge. Scale lines as marked.

RANGE AND HABITAT. Known only from Tamborine Mtn, SEQ (Fig. 5); in notophyll vine forest.

COMPARISONS. *C. parkini* sp. nov. can be distinguished from the sympatric rainforest-dwelling *Fastosarion aquila* (Cox, 1866) by its shell,

animal colour and skin texture. The latter species has a shell which is rounded with complete internal whorls and which has comparatively strong spiral sculpture. The animal of *F. aquila* has roughly textured skin, orange-brown colour, black spots on the shell lappets and mantle lobes,

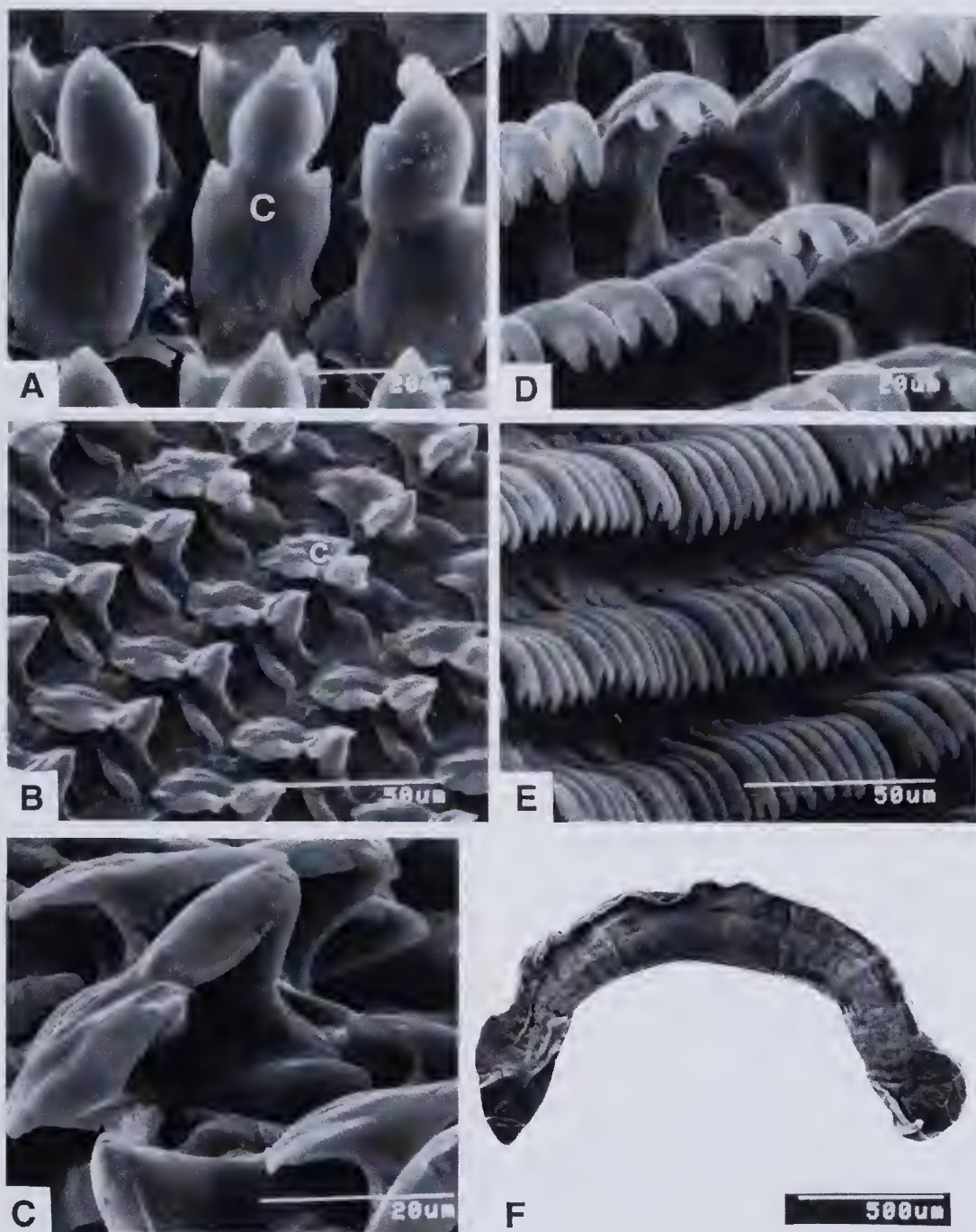


FIG. 4. Radula and jaw of *Cucullarion parkini* sp. nov., paratype, QMMO20858. A, central (marked c) and inner lateral teeth. B, central (marked c) and inner lateral teeth showing basal plate and interrow support. C, close-up of lateral tooth showing basal plate and interrow support mechanism (note cusp wear). D, inner marginal teeth (note frenal tricuspid in centre). E, outer marginal teeth. F, jaw. Scale lines as marked.

and orange outer margins on the sole of the foot (whitish in *C. parkini*). *F. virens* (Pfeiffer, 1849)

occurs in rainforest on Tamborine Mtn but can also be found in wet sclerophyll forest. The ani-

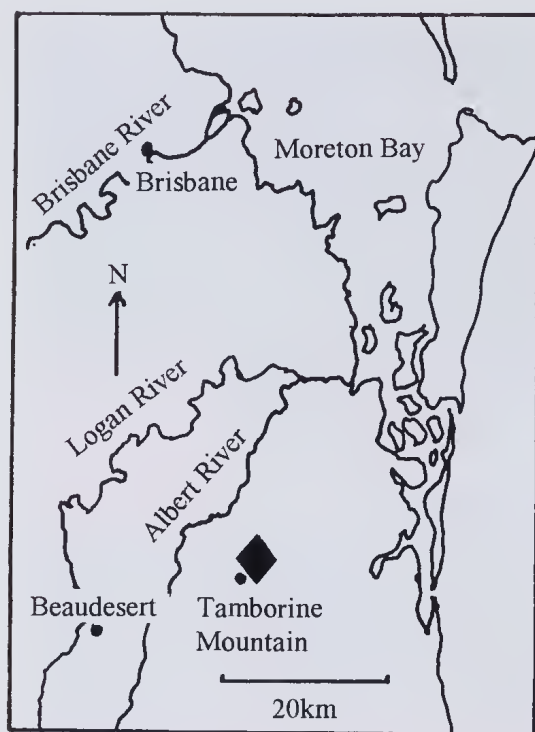


FIG. 5. Type locality of *Cucullarion parkini* sp. nov. (◆).

mal of this species is smooth externally, pinkish-grey in colour with pink to red outer margins on the sole of the foot. The shell of *F. virens* has complete internal whorls and fine spiral sculpture (Stanisic, 1995).

The radular teeth of *C. parkini* do not differ greatly in structure from those of other species of semi-slug examined by the author (Stanisic, 1993a, b). Most variability in the radula of these species appears to occur in the relative numbers of lateral and marginal teeth. In this respect *C. parkini* is most similar to *Eungarion mcdonaldii* Stanisic, 1993 from the rainforests of the highlands W of Mackay, MEQ which also has few laterals and a very large number of marginals. However, as suggested by Stanisic (1993b), these teeth counts may merely reflect similarity in feeding preferences.

REMARKS. *C. parkini* sp. nov. is a relatively rare native land snail. Only a single lot of live individuals has been collected from the trunks of palm trees on Tamborine Mtn even though this locality has been a much-visited collecting spot during the author's 17 year tenure at the QM. Previously only one shell existed in a private collection which was acquired by the Museum in 1989. The

live specimens were collected during a thunderstorm when they emerged from among the roots of palm trees.

The sleek form and beige colour of the animal of *C. parkini* is an unusual combination of features among the many species of often large and colourful semi-slugs present in eastern Australia (Stanisic, unpubl.).

DISCUSSION

The reduction in the internal whorls of *C. parkini* is similar to that seen in the MEQ and NEQ species, *Thularion semoni* Stanisic, 1993, *E. mcdonaldii* Stanisic, 1993 and *Parmacochlea fisheri* Smith, 1884 (see Hedley, 1893; Stanisic, 1993a, b). Stanisic (1993a) suggested that such species of semi-slug have a more acute sensitivity to environmental moisture levels than those with less reduced shells. However, the relationships of *C. parkini* are not immediately obvious because major anatomical differences between the aforementioned species and *C. parkini* suggest that the similarity in the degree of shell reduction is probably due to convergence among species which have independently become adapted to particularly moist environments. *C. parkini* may be a derivative of a more completely shelled local ancestor in which case the lineage may also include other local extant species such as *F. aquila* and *F. virens*. However, anatomical data (Stanisic, unpubl.) suggest that any relationship between these species and *C. parkini* is also distant.

Alternatively, *C. parkini* might be a remnant of a once more widespread group of colonisers which already had reduced shells and which were adapted to areas of high rainfall. Such conditions could have been present even in much of the lowlands in eastern Australia in the Oligocene and Miocene (Galloway & Kemp, 1981; Kemp, 1981). Subsequent shift in climate to a drier regime restricted these rainforest habitats to upland and montane refugia which were able to maintain high and stable moisture levels either through rainfall or cloud-drip. If the ancestors of *C. parkini* were specialised for this wet environment then they too would have been restricted to a series of upland rainforest fragments. In these circumstances it would be reasonable to expect that any other potential remnants of that group might also now occur in wetter mountain-top habitats.

Evidence from palynological studies suggests that major shifts in the extent of rainforest along the east coast of Australia have taken place in the Pleistocene and in particular since the last inter-

glacial i.e., 120,000 years ago (Hopkins et al., 1996; A.P. Kershaw, 1985; A.P. Kershaw et al., 1991). On a number of occasions during this period rainforest was restricted to small, perennially moist refugia such as mountain tops. Although these conclusions were based on core samples from SE Australia and NE Queensland, it might not be unreasonable to expect that they also have applicability to the rainforests of the Border Ranges. This region includes a number of montane refugia which would have provided suitable stable moisture regimes for the persistence of rainforest. The rainforests of the Darlington Ra. are only small outliers of this massif and it would not be an altogether unexpected discovery if close relatives of *C. parkini* are found in the higher reaches of the MacPherson Ranges where rainforest is even more extensive.

The common name 'Hooded Semi-slug' is proposed for this species.

ACKNOWLEDGEMENTS

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TEMPORENA IREDALE UNRAVELLED. *Memoirs of the Queensland Museum* 42(2): 604, 1998:- Iredale (1933) erected *Temporena* as a subgenus of *Gnarosophia* Iredale, 1933 to accommodate a large striped camaenid, *Helix whartoni* Cox, 1871 from Holbourne I., off Bowen, mideastern Qld (Fig. 1). *Gnarosophia* also included a number of large camaenids from the Wet Tropics Biogeographic Region as well as *G. mitifica* Iredale, 1933 (=nom. nov. for *Helix incei* var. *multifasciata* Cox, 1864 non Weinland & Anton, 1857) (Fig. 2). In his original description Cox (1864) recorded the locality of *G. mitifica* as 'Marked. Cape York', which in the context of that publication suggested that he was suspicious of its origins because for all other entries the locality was given without qualification. Subsequently, Cox (1868) figured this specimen as a large form of *Helix incei* Pfeiffer (1845) (confirmed on one of the specimen labels in Cox's handwriting) and at that stage considered that it came from Wide Bay, SE Qld. Presumably because he felt that it was conspecific with a similar looking shell, a form of *H. incei*, which was then considered to come from this area (Cox, 1868). This Wide Bay species was later described as *Helix bayensis* Brazier, 1875. Cox (1909) synonymised his *multifasciata* with *H. bayensis* (as confirmed by a corrected specimen identification label in Cox's handwriting), however, Iredale (1933) considered that *G. mitifica* was a distinct species related to *T. whartoni*.

Iredale (1937) raised *Temporena* to generic rank and also included the poorly localised *G. mitifica*. More recently Smith (1992) regarded *G. mitifica* as conspecific with *T. whartoni* and also synonymised *Temporena* with a convenient portmanteau taxon, *Sphaerospira* Mörchl, 1867. However, Stanisic (1996a, b) alluded to the probable polyphyletic make-up of *Sphaerospira* sensu Smith, 1992 and discussed the basis for a complete revision of the group.

An analysis of shell microsculpture and reproductive anatomy of these species which was undertaken by the author shows that *Temporena whartoni* has a shell sculptured with very fine and extremely crowded, radial periostracal wrinkles. The animal has a penis which internally possesses a verge, single longitudinal pilaster and densely scattered pustules apically and fine longitudinal ridges basally. Examination of the periostracal microsculpture of the holotype of *G. mitifica* reveals relatively gross, comparatively widely separated and obliquely disposed ridglets (as opposed to the fine, almost axial, crowded ridglets in *Temporena*) and is typical of that found in the large striped camaenids which occur between Townsville and Cardwell, NE Qld. Comparison of type of *G. mitifica* with shells in the Queensland Museum indicates that it actually comes from the Palm Is, north-east of Townsville. The penis interior of this latter group of species has a more complicated pilaster pattern than that seen in *Temporena*

(Stanisic, unpubl.). These differences are considered by the author sufficient not only to identify these camaenids as separate species but also to warrant their generic separation.

A study of additional material in the Queensland Museum reveals that *Temporena* comprises a relatively large group of species characterised by variously striped shells which all have fine periostracal sculpture and internal penial morphology similar to that of *T. whartoni*. These species are distributed south of the Townsville-Cardwell group of large camaenids between Longford Ck. N of Proserpine and Cape Upstart, SE of Ayr, mideastern Qld. The type species is confined to Holbourne I.

The convoluted nature of this taxonomic odyssey has resulted from past reliance on shell size, shape and colour pattern for separating both genera and species within the group of large striped Qld camaenids. This has led to a classification which is flawed by the failure to recognise the intraspecific variability of species in size, shape and colour pattern of the shell as well as convergences in these characters between often distantly related species. The confusion is poignantly illustrated by the fact that one of two paratypes of Cox's *multifasciata* in the Australian Museum (AMSC107645) is a specimen of *T. whartoni*.

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 J. Stanisic, *Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 5 May 1998.*



Fig. 1. *Helix whartoni* Cox, 1871. Holotype, BMNH1880.12.11.6.



Fig. 2. *Gnarosophia mitifica* Iredale, 1933. Holotype, AMSC100628.

REVISION OF THE PLIOCENE DASYURID, *DASYURUS DUNMALLI*
(DASYURIDAE: MARSUPIALIA)

STEPHEN WROE AND BRIAN S. MACKNESS

Wroe, S. & Mackness, B.S. 1998 06 29: Revision of the Pliocene dasyurid, *Dasyurus dunmalli* (Dasyuridae: Marsupialia). *Memoirs of the Queensland Museum* 42(2): 605-612. Brisbane. ISSN 0079-8835.

The discovery of well-preserved material referable to *Dasyurus dunmalli*, from Chinchilla and Bluff Downs Local Faunas, has provided diagnostic characters enabling the distinction of this taxon from all extant species of *Dasyurus* on the basis of molar morphology alone. Parsimony analysis places *D. dunmalli* as the sister taxon to *D. maculatus*, but requires the acceptance of considerable homoplasy. These two taxa form a monophyletic clade together with *D. albopunctatus* and *D. spartacus*, supporting the proposition that these two New Guinean quolls do not share a special relationship with *D. hallucatus*. □ *Dasyuridae*, *Dasyurus dunmalli*, molar morphology, parsimony analysis, Pliocene, Queensland.

Steve Wroe & Brian Mackness, School of Biological Sciences, University of New South Wales 2052, Australia; 28 June 1997.

Dasyurus (Geoffroy, 1796) contains a group of marsupicarnivores known as quolls found in both Australia and Papua New Guinea. There are six extant species — the New Guinea Quoll, *D. albopunctatus* Schlegel, 1880; the Western Quoll, *D. geoffroii* Gould, 1841; the Northern Quoll, *D. hallucatus* Gould, 1842; the Tiger Quoll, *D. maculatus* (Kerr, 1792); the Bronze Quoll, *D. spartacus* Van Dyck, 1987 and the Eastern Quoll *D. viverrinus* (Shaw, 1800).

A number of fossil species, other than *D. dunmalli*, have been referred to *Dasyurus*. McCoy (1865) described *D. affinis* from the Holocene Bone Cave, in Bone Cave Ravine at the head of Toolam Toolern Ck near Gisborne in Vic. Mahoney (1964) synonymised *D. affinis* with the extant *D. maculatus*. Owen (1877) described *D. mordax* from an unspecified cave in Australia. The holotype is now missing (Mahoney & Ride 1975) and Archer (1982a) suggested that the specimen was pathological. The status of this taxon is regarded as doubtful. *Dasyurus bowlingi* Spencer & Kershaw, 1910 was described from King Is. in Bass Strait. This specimen was later referred to *D. maculatus* by Marshall & Hope (1973).

Dasyurus dunmalli Bartholomai, 1971 now represents the only extinct species of *Dasyurus*. The original description was based on three worn specimens from the Pliocene Chinchilla Sands Local Fauna. Archer (1982a) tentatively referred another specimen (AMF62530) from the Pliocene Bow Local Fauna to *D. dunmalli*. Other fossil *Dasyurus* include a number of specimens from the Plio-Pleistocene Floraville Local fauna

which Archer (1982a) was unable to assign past generic level.

The unravelling of relationships within *Dasyurus* has been the focus of some attention in recent years. Historically, *D. hallucatus* and *D. albopunctatus* have been treated as monophyletic and placed in a separate genus, *Satanellus* (Pocock, 1926; Tate, 1947; Troughton, 1967; Archer, 1982a), with monophyly for these two species based on geographic proximity and the shared characters of small size and spots. In a morphology-based review of intrageneric relationships, Van Dyck (1987) suggested that *D. albopunctatus* and the newly described Bronze Quoll *D. spartacus* were in fact specialised taxa which, together with *D. dunmalli*, formed the sister clade to *D. maculatus*.

Molecular evidence has largely sustained Van Dyck's argument against monophyly for *D. hallucatus* and *D. albopunctatus* (Kirsch et al., 1990; Krajewski et al., 1994), but otherwise the elucidation of intrageneric relationships remains contentious. On the basis of DNA/DNA hybridisation studies, which included three species of *Dasyurus*, Kirsch et al. (1990) found *D. albopunctatus* to be more closely allied to *D. maculatus* than *D. hallucatus*. Krajewski et al. (1994), from an analysis of cytochrome *b* data, with all extant *Dasyurus* except *D. geoffroii* represented, likewise inferred polyphyly for the *Satanellus* of Tate (1947) and Archer (1982a), but treated *D. albopunctatus* as monophyletic with *D. spartacus* and *D. viverrinus*, a relationship supported by high bootstrap values. However, the position of *D. hallucatus* within Dasyurinae was

very poorly resolved, as was the phylogeny of dasyurines in general. Interestingly, in the same study, strong support was forwarded for a special relationship between *D. maculatus* and *Sarcophilus harrisii*. Monophyly for these two most specialised of modern dasyurid carnivores has been tentatively proposed by previous authors (Ride, 1964; Archer, 1982a), on the basis of a demonstrable structural morphocline incorporating the Pliocene *Glaucodon ballaratensis*. However, some results generated from the cytochrome *b* data of Krajewski et al., (1994), such as strong support for monophyly and *Pseudantechinus ningbing* and *Myoictis melas*, are extremely difficult to reconcile with morphological data and may signal the need for caution in interpretation.

In this paper the position of *D. dunmalli* within *Dasyurus* is re-examined with the benefit of additional data from five new, well-preserved dentary fragments from the type locality as well as two isolated molars, from the early Pliocene Bluff Downs Local Fauna referred to *D. dunmalli*.

MATERIALS AND METHODS

Character-state polarities follow those used by Van Dyck (1987) and Archer (1976). Character state distributions are shown in Table 1. Phylogenetic analysis was applied using PAUP 3.0 (Swofford, 1993). Wagner analysis was performed using the 'exhaustive' algorithm with multistate characters treated as ordered. DELTRAN character optimisation was used to distinguish the most parsimonious array of transformations. The evolutionary transformation of characters is delayed when the DELTRAN option is applied, pushing them up the tree and effectively favouring parallelisms over reversals where there is an equally parsimonious choice (Wiley et al., 1991). The use of this option was considered prudent as much of the data set for *D. dunmalli* was missing. The DELTRAN optimisation includes transformations for missing data at the minimal level, allowing for the possibility that a transformation might have evolved at a lower point on the tree (Simmons, 1993; Novacek et al., 1988).

Bootstrap analysis, considered an alternative for the problem of small data sets (Felsenstein, 1985; Potvin & Roff, 1993), was undertaken with a branch and bound search and one thousand replications.

The identification and treatment of character complexes are common dilemmas in phylogenetic analyses (Kluge & Farris, 1969; Archer, 1982b; Simmons, 1993). Character transformations in the upper dentitions often reflect predict-

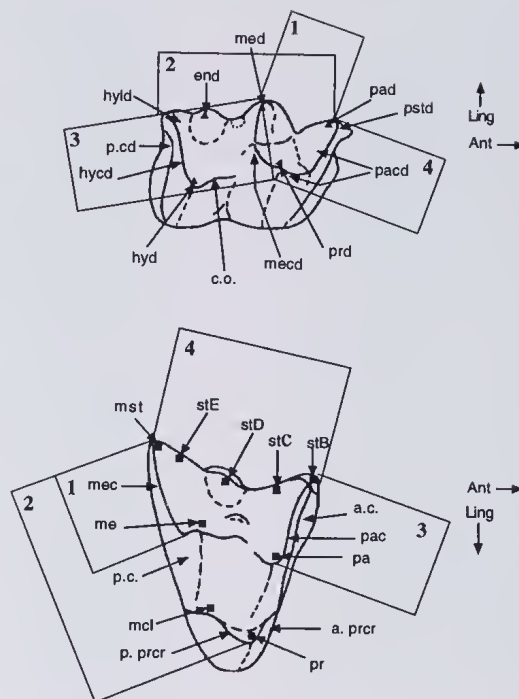


FIG. 1. Diagram showing terminology of morphology of an upper and lower molar of stylised dasyurid. Regions used for measurements in Table 2 are also shown. Arrow indicates anterior of molar. Abbreviations: a.c.=anterior cingulum; a.pcr=anterior protoecrista or preprotoecrista; co=cristid obliqua; end=entoconid; hycd=hypocristid; hyd=hypoconid; hyl=d=hypoconulid; mc=metaconid; mcl=metaconule; me=metacone; mecd=metacristid; med=metacristid; mst=metastylar corner of tooth; pa=paracone; pac=paracrista; pacd=paracristid; pad=paraconid; p.c.=posterior cingulum; p.cd=posterior cingulid; p.pcr=posterior protoecrista or postprotoecrista; pr=protocone; prd=protoconid; pstid=parastylid; stB=stylar cusp B; stC=stylar cusp C; stD=stylar cusp D; stE=stylar cusp E (after Archer, 1976, 1984a).

able changes in the lower dentitions and vice versa (e.g., postmetacrista length is correlated with paracristid length, protocone reduction with talonid reduction). For characters used in this analysis with a demonstrably direct structural link to counterparts in the upper or lower dentitions, only one of two possible 'characters' has been used (i.e., upper or lower).

Systematic terminology follows Kirsch & Calaby (1977) for *Dasyurus* and Wroe (1996, 1997 a,b) for higher level systematics of Dasyuro-morphia. Dental nomenclature is given in Fig. 1

TABLE 1. Data matrix showing the distribution of 22 characters for 7 *Dasyurus* species and a hypothetical ancestor that were analysed using the Wagner parsimony and bootstrap algorithms of PAUP 3.0. Character state codes: 0=pleisomorphic; 1=1st intermediate state; 2=2nd intermediate state; 3=most apomorphic state; ?=missing.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Hypothetical ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>D. hallucatus</i>	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0
<i>D. viverrinus</i>	1	1	1	1	0	2	1	2	1	2	1	1	0	1	0	1	1	0	0	1	2	1
<i>D. dunmalli</i>	?	?	?	1	1	?	0	?	?	?	?	?	0	0	1	2	?	?	?	?	?	?
<i>D. albopunctatus</i>	1	1	1	1	1	2	1	2	1	2	1	1	0	1	1	2	1	0	0	1	1	0
<i>D. spartacus</i>	1	1	1	1	1	2	1	2	1	2	1	1	0	1	1	2	1	1	1	1	1	0
<i>D. geoffroyi</i>	0	0	1	1	0	2	1	1	1	2	1	1	0	1	0	1	1	0	0	1	0	0
<i>D. maculatus</i>	1	1	1	1	1	2	1	3	1	2	2	1	1	0	1	3	0	0	0	1	1	0

and follows Flower (1867) and Luckett (1993) regarding the molar-premolar boundary, where the adult (unreduced) postcanine cheektooth formula of marsupials is P1-3 and M1-4. Luckett (1993) has suggested that in *D. viverrinus* it is P2, rather than P3, which is lost. This interpretation might also apply to other members of the genus. However, pending the publication of data based on more extensive sampling, we adhere to the conventional view that P3 represents the lost premolar position in *Dasyurus*. Measurements of tooth dimensions are presented in Table 2. The regions measured are shown in Fig. 1.

Institutional abbreviations. AM, Australian Museum; AR, Vertebrate Palaeontology Collection, University of New South Wales; QM, Queensland Museum; W, Wilkinson private collection.

SYSTEMATICS

Order DASYUROMORPHIA Gill, 1872

Superfamily DASYUROIDEA Goldfuss, 1820

Family DASYURIDAE Goldfuss, 1820

Genus *Dasyurus* Geoffroy, 1796

Dasyurus dunmalli Bartholomai, 1971
(Fig 2)

MATERIAL. HOLOTYPE: QMF6579, L mandibular ramus (partial), including base of C1, P1-3, M1-3, with M2-3 protoconid tips missing (adult). **OTHER MATERIAL:** QMF23227, R M² (partial); F23226, L M3 crown; AR74, L mandibular ramus (partial), including base of C1, P1-3, M1-3 (cast of holotype); AR73, R mandibular ramus (partial), including C1, P1-2, alveoli for P3, M1-3, M4 broken (cast of F742); F12682, L dentary fragment containing M2-3 and alveoli for P1-3, M1 and M4; F30477, L dentary fragment containing M1-2. W3357, R dentary fragment containing partial I1-2, roots for I3, C1 and P1, P2-3, and M1-2.

LOCALITY AND AGE. QMF6579, AR74, AR73, QMF12682 and F30477 are from the Chinchilla Local Fauna, Chinchilla Sand formation, Darling Downs, SEQ, considered to be early to middle Pliocene in age (Archer & Wade, 1976). F23227

and F23226 are from the Bluff Downs Local Fauna, NEQ, considered to be of early Pliocene age (Archer & Wade, 1976).

RE-DIAGNOSIS. A medium-sized species of *Dasyurus* that differs from other members of the genus in the retention of P3 and a less-crowded premolar row, and from all except *D. maculatus* in possessing well-developed posterior cingulids on M1-3. Differs from *D. hallucatus*, *D. geoffroyi* and *D. viverrinus* in possessing trigonids longer than talonids on M2, premolars which are ovate and large in occlusal view, more reduced metaconids and an M1 which is only slightly wider posteriorly than anteriorly. Differs from *D. viverrinus*, *D. albopunctatus*, *D. spartacus* and *D. maculatus* in having a cristid obliqua which terminates anteriorly in a more lingual position (almost directly beneath the carnassial notch of the metacristid on the unworn M3). Differs from *D. albopunctatus* and *D. maculatus* in showing less reduction of the metaconids. Differs from *D. maculatus* in lacking bulbous molars.

REVISED DESCRIPTION. *Lower dentition.* Characters not noted in the original description (Bartholomai, 1971) are: M1-3 metaconids are reduced and posteriorly displaced; the metacristids and hypocristids of M1-3 are angled away from the transverse axis of the dentary; the talonid is only slightly wider than the trigonid on M1; the dimension of M2 trigonid exceeds that of the talonid on the long axis; the M1-3 entoconids are small; a well defined posterior cingulid is observable on M1-3; the cristid obliqua terminates against the posterior face of the trigonid in an increasingly lingual position from M1-3 (almost directly beneath the carnassial notch of the M3 metacristid in unworn specimens).

Upper dentition. L M² (QMF23227). This is the only element of the upper dentition referred to *D. dunmalli* to date. The tooth is worn, with a region extending buccally from the protocone tip to include the basal portion of the paracone and

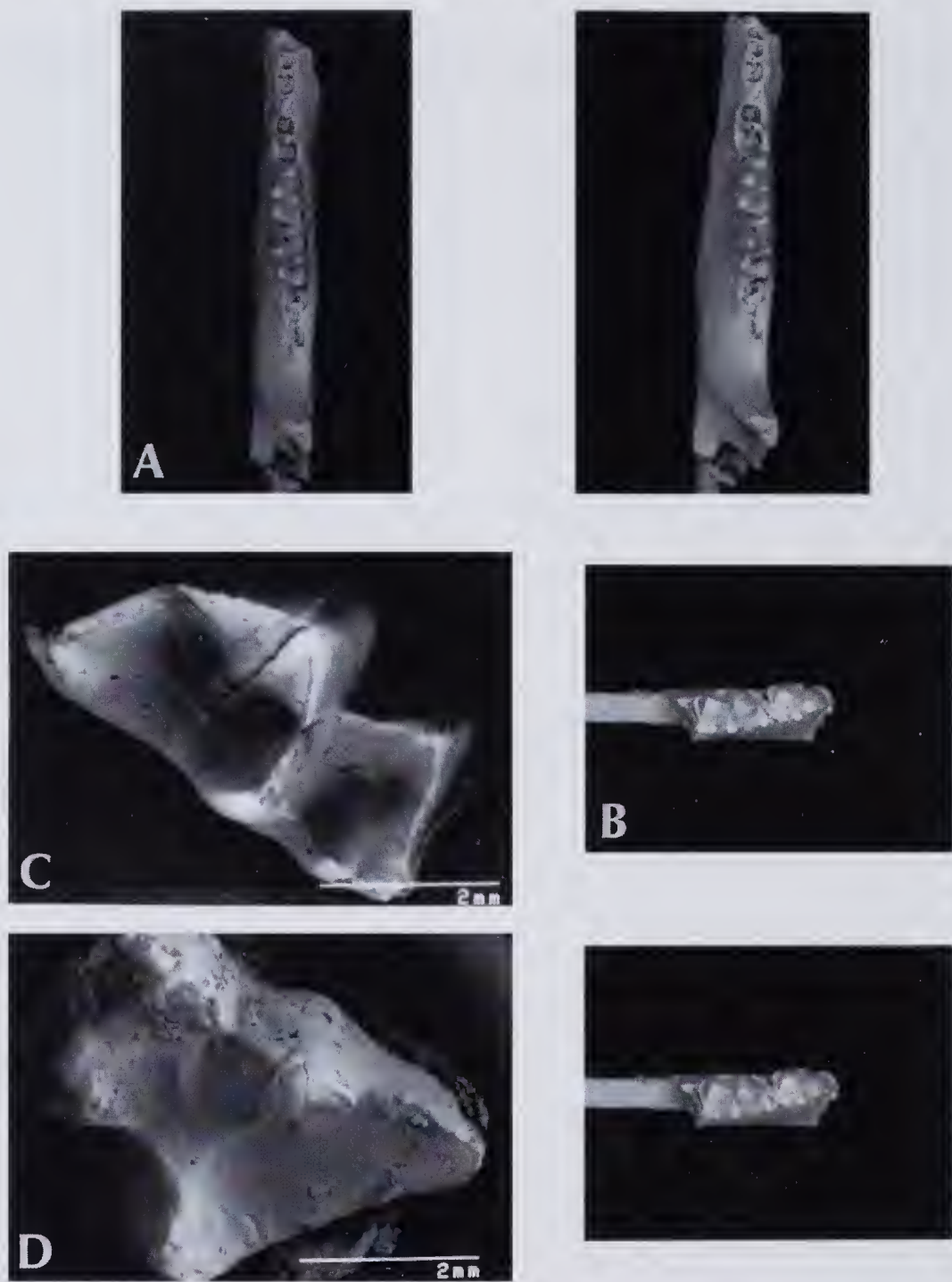


FIG. 2. *Dasyurus dunmalli*. A, QMF12682, L dentary fragment containing M₂₋₃ and alveoli for P₁₋₃, M₁ and M₄, stereo-pair in occlusal view; B, QMF30477, L dentary fragment containing M₁₋₂, stereo pair in occlusal view; C, QMF23226, L M₃ crown, occlusal view; D, QMF23227, R partial M₂, occlusal view.

TABLE 2. Tooth measurements of *Dasyurus dunmalli* in mm.

LOWER MOLARS	M1	M2		M3
QMF Number	30477	12682	30477	12682
Paraconid-metaconid	2.9	3.4	3.5	3.5
Paraconid-hypocoulid	4.5	5.5	5.4	5.8
Metaconid-protocoulid	2.2	3.4	2.9	3.4
Paraconid-protocoulid	2.5	3.8	3.9	3.9
UPPER MOLARS	M2			
QMF number	23227			
Metacone-metastylar corner	4.0			
Paracone-metastylar corner	2.6			
Parastylar corner-metastylar corner	5.0			

metacone missing (including the location of the protoconule and metaconule). In order of decreasing height, the principle cusps are; stylar cusp D, metacone, stylar cusp B, paracone, protocone, no stylar cusp C or E. Stylar cusp D is large and positioned about half way along the stylar shelf (equidistant between metacone and metastylar corner). Although broken, enough remains of the protocone to clearly establish its small size. In order of diminishing length, the principal vertical shearing crests are; postmetacrista, paracrista, premetacrista and postparacrista.

The postmetacrista is dominant, about three times the length of the paracrista. There is a very slight ectoflexus in the stylar shelf between stylar cusps B and D. A weakly defined anterior cingulum is present but no posterior cingulum is observable.

REMARKS. Three of the four new specimens referred here to *D. dunmalli* are almost completely unworn and reveal detail obscured or missing in previously described material. In the two partial dentaries (QMF30477 and QMF12682), from the same locality as the holotype, several characters are apparent which clearly distinguish *D. dunmalli* from unworn specimens of *D. viverrinus*. Posterior displacement of the metaconid in *D. dunmalli* is greater than in *D. viverrinus* and comparable with that of *D. maculatus*. This character is linked with torsion of the metacristid and hypocristid away from the transverse axis of the dentary, opening of the trigonid basin and possession of an M₂ trigonid which surpasses the talonid in the anteroposterior dimension in *D. dunmalli*. A well-defined posterior cingulid is observable on M₁₋₃ of QMF30477 and QMF12682. Although very worn on the holotype, this character is clearly visible on QMF740. In most extant *Dasyurus* spp, the posterior cingulid is greatly diminished or lost excepting some *D.*

maculatus. The lingual point of termination for the cristid obliqua against the posterior face of the trigonid further distinguishes *D. dunmalli* from *D. viverrinus* and is most similar to the condition seen in *D. hallucatus*. The unworn M3 from Bluff Downs has been assigned to *D. dunmalli* because it shows each of the characters mentioned above.

PHYLOGENETIC ANALYSIS

A single most parsimonious tree requiring 33 steps is produced by Wagner analysis (Fig 3). The tree shows a consistency index (CI) of 0.9.9, and a retention index (RI) of 9.03. Monophyly for *Dasyurus* is based on reduction in premolar occlusion, loss of P3, paracone reduction, diminution of the posterior cingulid and loss of the M₄ entoconid (characters 6,7,10,14 & 17; see Tables 2 & 3). Within the genus, *D. hallucatus* is the sister group to all other species of *Dasyurus*. Monophyly for *D. geoffroii*, *D. viverrinus*, *D. albopunctatus*, *D. spartacus*, *D. dunmalli* and *D. maculatus* is founded on possession of the following synapomorphies; a U-shaped premolar row, canine hypertrophy, a reduction in premolar shear, a relative increase in M₃ postmetacrista length, a metacone perpendicular to stylar cusp D, more closely approximated metacone and stylar cusp D (M₁₋₃), reduction of M₄, metaconid reduction and complex penile morphology (characters 3,4,6,8,9,10,11,12,16 & 20). Together *D. hallucatus* and *D. geoffroii* form a sister clade to *D. viverrinus*, *D. albopunctatus*, *D. spartacus*, *D. dunmalli* and *D. maculatus*, a clade defined by the following synapomorphies; lack of diastema between I¹⁻², I¹ not hypsodont relative to I², further hypertrophy of the M₃ postmetacrista and reduction of the hallux (characters 1,2,8 & 21). *Dasyurus albopunctatus*, *D. spartacus*, *D. dunmalli* and *D. maculatus* are united by possession of: larger more ovate premolars in occlusal view, trigonids, markedly larger than talonids on the long axis, and further reduction in metaconid size (characters 5,15 & 16). At this point an unresolved trichotomy is produced within *D. albopunctatus*, *D. spartacus* and a monophyletic *D. dunmalli* and *D. maculatus* clade. *Dasyurus dunmalli* and *D. maculatus* are united on the basis of a single feature, possession of a well defined posterior cingulid (character 14).

A tree of identical topography is generated by the bootstrapping algorithm (Fig. 3). Monophyly for a *D. geoffroii*, *D. viverrinus*, *D. albopunctatus*, *D. spartacus*, *D. dunmalli* and *D. maculatus* clade is supported in 95% of replications. Unity

DISCUSSION

Previous authors have justifiably exercised restraint when considering the phylogenetic position of *D. dunmalli*. Bartholomai (1971) found *D. dunmalli* to be structurally most similar to *D. viverrinus*. Archer (1982a) also found *D. dunmalli* to be morphologically closest to *D. viverrinus* but canvassed three phylogenetic scenarios: *D. dunmalli* was either ancestral to all modern *Dasyurus*, ancestral to all *Dasyurus* species except *D. hallucatus*, or it represented a separate lineage highly convergent on *Dasyurus*. *Dasyurus dunmalli* was considered a derived taxon within the genus by Van Dyck (1987) who proposed that *D. dunmalli* might be monophyletic with *D. spartacus* and *D. albopunctatus*.

The study of more recent and better preserved material has enabled the clear distinction of *D. dunmalli* from *D. viverrinus*, and all other species of *Dasyurus*, on molar morphology alone and extended its known geographical and chronological range. The phylogeny for *Dasyurus* supported in the present analysis concurs in some respects with that of Van Dyck (1987), as does the phylogeny generated for the genus *Dasyurus*. In both studies *D. dunmalli* is treated as part of a *D. albopunctatus*, *D. spartacus* and *D. maculatus* clade with no special relationship between the two New Guinean quolls and *D. hallucatus*. However, differences are apparent. In the present study, *D. albopunctatus*, *D. spartacus* and *D. dunmalli* + *D. maculatus* represent an unresolved trichotomy, whereas Van Dyck (1987) suggests that *D. dunmalli* is the sister taxon to the two New Guinean quolls and that together these three taxa form the sister taxon to *D. maculatus*. In addition, the positions of *D. viverrinus* and *D. geoffroii* in Fig. 3 are the reverse of those in the Van Dyck study.

Homoplasy features in all phylogenies incorporating *D. dunmalli* (Archer, 1982a; Van Dyck, 1987). In particular interpreting the significance of the small but distinct P₃ in this fossil taxon has vexed previous authors. The presence of P₃ is almost certainly plesiomorphic for *Dasyurus*. But because this tooth is not present in any other member of the genus and its presence in *D. dunmalli* requires either the acceptance of apomorphic reversal to a primitive state in *D. dunmalli*, or multiple convergent loss of P₃ within *Dasyurus* unless *dunmalli* is treated as the sister taxon to all other *Dasyurus* spp. Although the reappearance of a lost tooth within a lineage otherwise strongly influenced by selection for brachy-

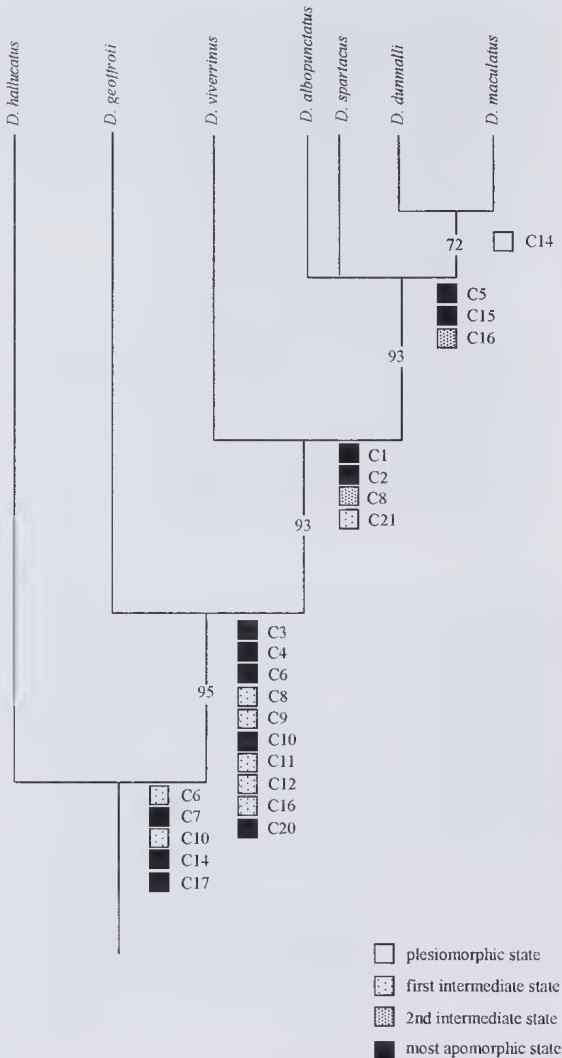


FIG. 3. Single most parsimonious cladogram for 7 species of *Dasyurus* and a hypothetical ancestor. Produced by Wagner and 50% majority rule consensus bootstrap analyses with character state changes for internal nodes. '?' indicate predicted occurrence of character states where the relevant material is unknown.

for a *D. viverrinus*, *D. albopunctatus*, *D. spartacus*, *D. dunmalli* and *D. maculatus* clade is sustained in 93% of replications. A *D. albopunctatus*, *D. spartacus*, *D. dunmalli* and *D. maculatus* clade is supported in 93% of replications. Weakest support is for monophyly of a *D. dunmalli*/*D. maculatus* clade which is sustained in 72% of replications.

TABLE 3. Characters and character states used in phylogenetic analysis with '0' representing the plesiomorphic state.

1. Presence of a diastema between I¹⁻². 0. present. 1. absent.
2. I1 morphology. 0. I¹ hypsodont relative to I2. 1. I1 not hypsodont to I2.
3. Shape of incisor row. 0. incisor row 'V'-shaped. 1. 'U'-shaped.
4. C1 morphology. 0. C1 proportionate. 1. C1 not proportionate.
5. Premolar morphology. 0. premolars narrow and small in occlusal view. 1. ovate and large in occlusal view.
6. Premolar occlusion. 0. premolars shear past each other in occlusion. 1. intermediate stage. 2. do not shear past each other in occlusion.
7. P3. 0. retained. 1. lost.
8. M3 metacrista length. 0. M3 shorter than for M2. 1. M3 and M2 about equal. 2. M3 longer than for M2. 3. M3 much longer than for M2.
9. Position of M¹ metacone relative to stylar cusp D. 0. perpendicular to stylar cusp D. 1. not perpendicular.
10. Paracone morphology. 0. Paracones not reduced. 1. intermediate stage. 2. greatly reduced.
11. Distance between metacone and stylar cusp D. 0. Metacone and stylar cusp D not approximated. 1. intermediate. 2. approximated.
12. M4 morphology. 0. M4 unreduced. 1. reduced.
13. Molar shape. 0. molars non-bulbous. 1. bulbous.
14. Posterior cingulid. 0. well developed. 1. diminished or lost.
15. M2 trigonid versus M2 talonid length. 0. lengths near equal. 1. M2 trigonid length clearly greater than talonid.
16. Metaconid size. 0. metaconid unreduced. 1. intermediate stage. 2. intermediate stage. 3. greatly reduced.
17. M4 morphology. 0. M4 with entoconid. 1. without entoconid.
18. Skull height. 0. low. 1. not low.
19. Rostrum breadth between lacrymals. 0. not broad. 1. broad.
20. Penile morphology. 0. Simple. 1. complex.
21. Hallux morphology. 0. hallux absent. 1. intermediate state. 2. most apomorphic state.
22. Hind foot morphology. 0. pes short and broad. 1. elongate.

cephalisation may be counterintuitive it is not unknown among mammalian carnivores (Kurten, 1988), but the identification of another plesiomorphy in *D. dunmalli*, i.e., a very well-developed posterior cingulid further complicates the issue. A need for circumspection is further stressed because many features are unknown for *D. dunmalli* and previous work, based on Miocene fossil material (Wroe, 1996; 1997a,b), has demonstrated unexpected complexity in the phylogeny of Dasyuromorphia. Nonetheless, results of the present study clearly show that reversal to a plesiomorphic state for both these features in *D. dunmalli* is the most parsimonious interpretation on the basis of available evidence.

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AUSTRALIAN POPULATIONS OF THE *NACTUS PELAGICUS* COMPLEX (REPTILIA: GEKKONIDAE)

GEORGE R. ZUG

Zug, G.R. 1998 06 29: Australian populations of the *Nactus pelagicus* complex (Reptilia: Gekkonidae). *Memoirs of the Queensland Museum* 42(2): 613-626. Brisbane. ISSN 0079-8835.

An analysis of morphometric traits and scalation reveals that the Australian populations of the *Nactus pelagicus* complex differ from all other complex members by the presence of smooth subcaudal scales. This unique trait indicates that Australian *Nactus* represent a distinct clade from the New Guinea and Oceania populations. Other features of scalation (number of prelocaal pores, presence/absence of femoral pores) suggest that the northern and southern populations are distinct from one another. For these two groups, *Heteronota eboracensis* Macleay is available for the northern species and *Gymnodactylus cheverti* Boulenger for the southern one. □ *Reptilia, Squamata, Gekkonidae, Cape York Peninsula, geographic variation.*

G.R. Zug, Department of Vertebrate Zoology/mrc162, National Museum of Natural History, Washington, DC 20560, USA; 23 August 1997.

Two species of *Nactus* are known to occur in Australia. Both are confined to Cape York Peninsula (CYP). The recently discovered *Nactus galgajuga* is restricted to the boulder fields of the Trevathan Mtn Ra. (Ingram, 1978). In contrast, the second species is broadly distributed on the peninsula from the Cairns area to the Torres Strait Is (Fig. 1). Until recently, the widespread Australian *Nactus* was known as *N. pelagicus*; however, *pelagicus* is the proper name for the unisexual populations of *Nactus* occurring in Oceania (Zug & Moon, 1995).

The bisexual populations of Vanuatu, Solomon Is, New Guinea and its satellite island groups, and Australia have a number of available names. If these bisexual populations represented a single species, name assignment would be a simple matter of priority of publication. Moritz (1987), however, showed that several bisexual species exist. Among his six bisexual samples from Australia, Papua-New Guinea (PNG) and Vanuatu, he delineated three population-groups (Australia, PNG, Vanuatu) with different karyotypes and molecular traits. A preliminary morphometric and scalation survey across the entire range of *Nactus pelagicus* sensu lato indicated that several populations were morphologically distinct from one another and that at least three morphotypes occur in New Guinea (Moon & Zug, unpublished data). Zug & Moon (1995) compared the unisexual populations of Oceania to the adjacent bisexual populations of Vanuatu and the Solomon Is and showed that the bisexual populations were morphologically distinct and warrant recogni-

tion. The specific name *multicarinatus* Günther is available for this species.

The preliminary analysis also revealed that Australian populations were morphologically distinct from those of PNG. This observation was not unexpected, because Moritz (1987) had shown the Australian population to be karyotypically and biochemically distinct. Further, Greer (1989: 71) had suggested that two allopatric and morphologically distinct populations exist in Australia, a northern one separated from the southern 'in the vicinity of Princess Charlotte Bay'. Here, I offer an analysis of intra- and inter-population variation among CYP populations and confirm the existence of two species.

MATERIALS AND METHODS

Specimens of *Nactus pelagicus* sensu lato were examined from throughout CYP, the Torres Strait Is, and adjacent Fly R. floodplain of PNG (Fig. 1). Most specimens were grouped into local samples representing discrete geographic areas, usually 30km or less in diameter. The major sample localities (n > 10 adults) are (N to S; also see Fig. 1 & Appendix: 1): PNGW, Fly R. delta, mainly in vicinity of Emeti; TORR, southern Torres Strait Is; SOMER, Somerset at tip of CYP and localities immediately to the S; MAPO, Mapoon; WEIPA, Weipa; IRON, Iron Ra.; WENL, Wenlock; MCIL, McIlwraith Ra.; COOKT, Cooktown; CHIL1, CHIL2, Chillagoe. Minor sample localities (n < 10) include (N to S): VRIL, Vrilya Pt; NOAL, N Alice R. crossing; HORSE, Horse Trailer W. H.; FLIN, Flinders I. group; NYMPH, Nymph I.; LAURA, Laura;

MTCAR1, MTCAR2, Mt Carbine; TINA, Tinaroo; DUNK1, DUNK2, Dunk 1.; and the TYPES, Endeavour R. and Fitzroy I. I also examined but did not record complete data for individuals from other Australian localities to ensure that these individuals match the characteristics of individuals in nearby samples.

The data set consists of 11 mensural and 18 scalation characters (Table 1). These characters represent a reduced data set from the set used in the study of the Oceania, Vanuatu and Solomons populations (Zug & Moon, 1995), with uninformative characters and ones with high recorder error (inconsistency) being deleted. Other characters have been modified or added. These are: MENSURAL – Eye Diameter (redefined), Interorbital Distance; MERISTIC – Femoral Pores, Femoral-Precloacal Pore Series Contact, Postmental-Infralabial Contact, Postmental Scale Size, Subcaudal Scales, Tubercle Density on Thigh. Eye diameter (EyeD) is the greatest horizontal distance across the exposed eyeball. Interorbital distance (Interorb) is the transverse distance between the anterior edges of the orbits. Femoral pores (FemPor) is the total number of femoral pores on the left and right thighs. For both femoral and precloacal pores, I recorded only the pores perforating their scales as shown by a secretion plug. Pore contact (PoreC) indicates whether the femoral and precloacal pores form a continuous series. Postmental-infralabial contact (PmLab) is the number of scale rows between the enlarged postmental and the infralabial scales and has several states: in contact, no scale rows separating postmental and infralabials (0); one scale row separating them (1); two scales rows separating them (2); etc. Postmental scale size (Postm) is the area of the right postmental, expressed as the number of chin scales occupying an equivalent area and is always expressed as an even integer. Subcaudal scales (Subcaud) is the presence (0) or absence of keels (1) on the scales of the ventral surface of the unregenerated tail. Tubercle density on thigh (TubDens) is the relative density of enlarged tubercles on the anterodorsal surface of the thigh and has three states: no or widely spaced small tubercles (0); a few widely spaced enlarged tubercles (1); many, often nearly abutting, enlarged tubercles (2). The abbreviated names in Zug & Moon (1995) for these characters have been expanded to improve recognition within the text; the original abbreviations are identified in Table 1.

The condition of bilaterally symmetrical characters on the right side (unless damaged) was recorded. Measurements were taken with dial

TABLE 1. Character set for members of the *Nactus pelagicus* complex. Previous characters are synonyms of the character names from Zug & Moon (1995). Definitions as in Zug & Moon, 1995: table 1. Modified (*) and new characters are defined in the text.

Abbreviation	Character	Previous character
Measurements		
EyeD	Eye diameter	*ORD
HeadH	Head height	HH
HeadL	Head length	HL
HeadW	Head width	HW
Interorb	Interorbital distance	new
NarEye	Nares to orbit distance	NAOR
NeckL	Neck length	NL
SnForel	Snout to forelimb distance	SFL
SVL	Snout-vent length	SVL
SnW	Snout width	SW
TrunkL	Trunk or body length	BL
Scalation		
CloacS	Cloacal spurs	CS
CST	Cloacal spur's tip	CST
DorsTub	Rows of dorsal tubercles	DTR
FemPor	Femoral pores	new
ForefL	Forefoot lamellae	FFL
HindfL	Hindfoot lamellae	HFL
Inflab	Infralabial scales	IL
Palm	Palm scales	SCP
PmLab	Postmental-infralabial contact	new
PoreC	Femoral and precloacal pores continuous	new
Postm	Postmental scale size	new
PreciPor	Precloacal pores	PRCP
Subcaud	Subcaudal scales	new
Suplab	Supralabial scales	SL
TubRow	Tubercles in a parasagittal tubercle row	TR
TubHip	Tubercle rows over hips	DTH
TubHindl	Tubercle distribution on hindlimb	THL
TubDens	Tubercle density on thigh	new

calipers to the nearest 0.1 mm. Examination of the gonads revealed sex and maturity. Mature ♀♀ possess vitellogenic follicles >1.5 mm, oviducal eggs, or stretched oviducts; mature ♂♂ have enlarged testes and epididymides. The presence or absence of functional precloacal pores cannot be used to determine maturity because these pores are absent in adult ♂♂ of some Australian populations.

SYSTAT modules were used (DOS ver. 5.0 & Windows ver. 6.0.1) for the statistical analyses. Intrasample comparisons for identification of sexually dimorphic characteristics relied on the Bartlett's test for homogeneity of variance and the Student's t-test for equality of means. These same tests were used for examining the variation between samples and were complemented by



FIG. 1. Geographic occurrence of the *Nactus pelagicus* complex members in Australia and the location of sample localities for this study. ● = museum-vouchered specimen. Locality abbreviations explained in the text and in Appendix 1. Wellesley Is record (Bauer, 1994: map 40) is unconfirmed.

multivariate analyses. Principal Components Analysis (PCA) examines and estimates levels of phenetic similarities among the samples and potentially discerns patterns of geographic variation. The PCA covariance matrices derived from transformed (natural logarithms) for the mensural characters and raw data for scalation. Discriminate Function Analysis (DFA) assists in the identification of character(s) defining the a priori groups and possibly reveals mis-identified individuals. In the multivariate analyses, I used only specimens with complete data, and the mensural and meristic character sets were examined separately. Only seven localities had samples with sufficient adult geckos for a meaningful examination of sexual dimorphism: COOKT $n = 16$ ♀♀,

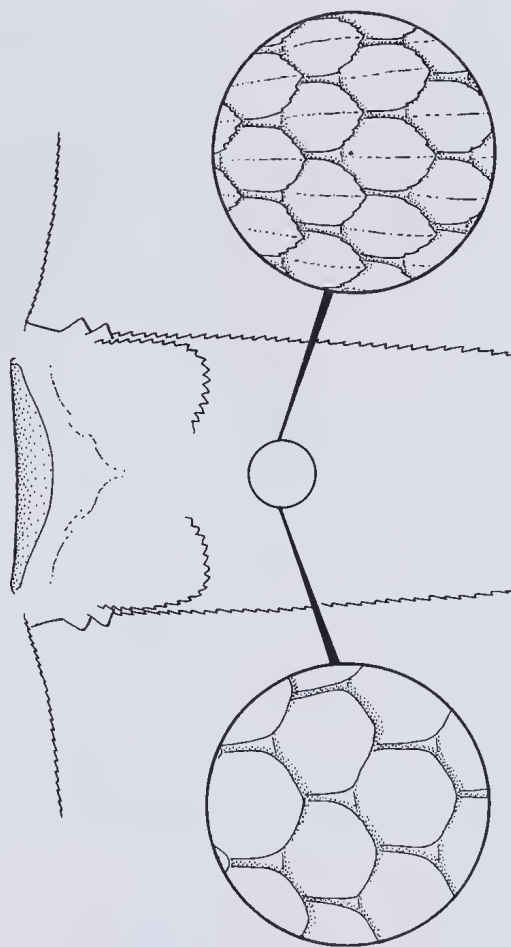


FIG. 2. Ventral view of the tail in *Nactus pelagicus* complex showing schematically two types of subcaudal scales, smooth (lower) and keeled (upper).

17 ♂♂; IRON $n = 8, 12$; MCIL $n = 5, 18$; PNGW $n = 13, 11$; SOMER $n = 11, 17$; TORR $n = 13, 6$; WEIPA $n = 16, 16$.

Statistical comparison proceeded in a step-wise fashion: 1) to test for sexual dimorphism; 2) to determine the nature and level of intrapopulational variation and variation among neighbouring samples; 3) to search for regional patterns of concordant and/or discordant variation, to identify speciation of populations. Mensural traits were compared only among adults; all ages were used for comparison of meristic traits.

RESULTS

SCALATION. *Sexual variation.* The presence of functional precloacal and/or femoral pores marks maturity in the ♂♂ of many gecko species, and

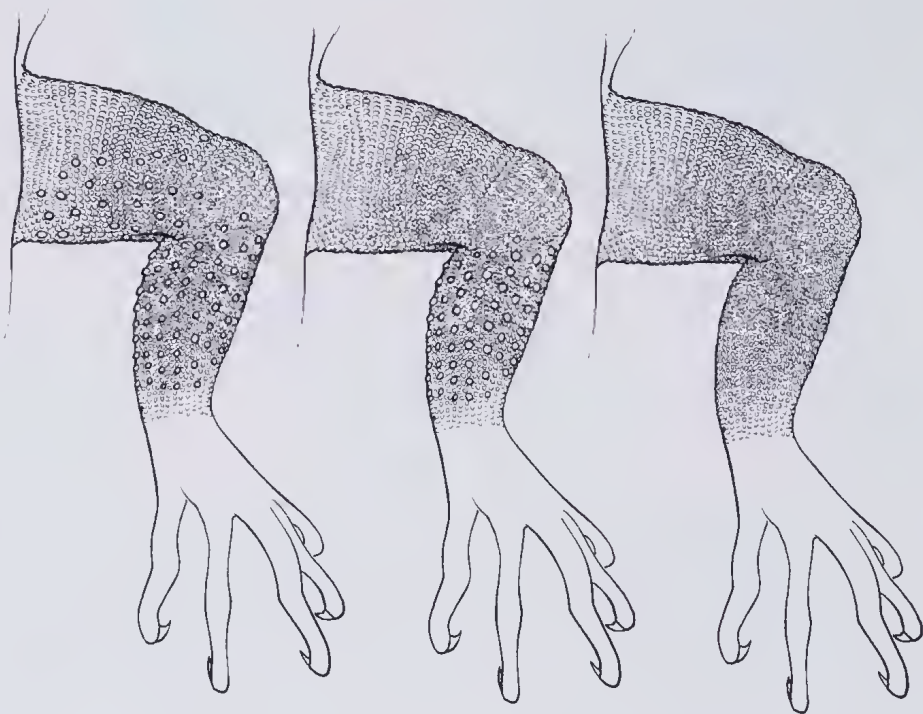


FIG. 3. Dorsal surface of the hindlimb depicting schematically the three states of hindlimb tuberculation: tuberculate (left), naked thigh (center), and atuberculate (right).

these pores are commonly absent in adult ♀♀. The pattern of occurrence in the Australian *Nactus* samples is variable for precloacal and femoral pores, and pores are not a reliable indicator of maturity. Functional precloacal pores occur in all mature PNGW, TORR, WEIPA, HORSE, MTCAR1, MTCAR2 and CAIR ♂♂. Active pores occur in some ♂♂ from the SOMER (88%), VRIL (50%), MAPO (30%), NOAL (75%), IRON (83%), WENL (50%), MCIL (94%), FLIND (40%), COOKT (47%), CHILI (33%) and DUNK1 (33%) samples. Mature ♂♂ from CHIL2 and TINA lack functional pores. In the northern sample (MCIL and northward), the number of active pores is typically six or more; whereas in the southern samples, ♂♂ seldom have more than three functional pores. Also an occasional adult ♀ in a few northern samples (TORR [AMSR44241], WENL [AMSR-105345]) possesses precloacal pores although usually fewer pores than ♂♂.

Femoral pores occur in some ♂♂ of the TORR (50%), SOMER (24%), NOAL (75%), WEIPA

(56%), IRON (33%), HORSE (100%) and MCIL (11%) samples, and in one specimen each of the ♀ TORR (AMSR44241) and WEIPA (AMSR82395) samples. All adult ♂♂ of the PNGW sample and of the Australian samples S of and including FLIND lack femoral pores. ♂♂ in the northern VRIL, MAPO and WENL samples lack femoral pores. When present, femoral pores lie distally on the thighs, seldom more than three or four on each side, and commonly bilaterally asymmetrical. Because femoral pores are absent or distally placed, PoreC is not used in the subsequent analyses.

In the six larger Australian samples, there are no significant sexual differences in scalation, aside from the presence or absence of pores, in the TORR and MCIL samples; only CST (mean = 0.50, 0.05; ♀♀, ♂♂) in SOMER, TubRow (mean = 25.1, 28.7) and Palm (mean = 5.8, 5.2) in WEIPA, TubDens (mean = 0.62, 0.08) in IRON, and Suplab (mean = 3.4, 3.1) in COOKT are significantly different ($p < 0.05$) between the sexes. All characters, except CST, in these samples

TABLE 2. Summary of variation in the scale characters of the Australian *Nactus pelagicus* complex. n = sample size. See Table 1 for character abbreviations and Appendix 2 for a summary of scalation by sample locality.

	Suplab	Inflab	Postm	PnLab	DorsTub	TubRow	TubHip
n	273	273	272	272	273	272	272
Mean $\pm$ SD	3.3 $\pm$ 0.44	2.9 $\pm$ 0.50	13.4 $\pm$ 3.83	0.01 $\pm$ 0.12	14.2 $\pm$ 1.05	22.9 $\pm$ 4.96	8.0 $\pm$ 0.53
Range	3-4	2-4	2-26	0-1	11-18	15-37	4-12
Coef Var (%)	13.5	16.9	28.7	820	7.4	28.7	6.7
	TubHindl	TubDens	CloacS	CST	ForefL	HindfL	Palm
n	272	239	272	268	272	269	272
Mean $\pm$ SD	1.9 $\pm$ 0.33	0.2 $\pm$ 0.36	1.6 $\pm$ 0.52	0.1 $\pm$ 0.34	14.2 $\pm$ 1.02	18.2 $\pm$ 1.29	5.3 $\pm$ 0.86
Range	1-2	0-1	0-3	0-1	11-18	14-23	3-8
Coef Var (%)	17.7	238	32.8	258	7.2	7.1	16.2

display a homogeneity of variance between the sexes. The PNGW $\delta\delta$ and $\eta\eta$ are similar in all scalation characters.

Because most characters are not sexually dimorphic and the few showing dimorphism are unique to a specific locality, scalation, with the exception of the pore traits, is assumed to be sexually monomorphic in the Australian *Nactus pelagicus* complex. Subsequent geographic analysis of scalation includes individuals of all ages and sexes in each locality sample; pore number (FemPor, PreclPor) is excluded from some analyses.

Geographic variation. All Australian *Nactus* (including *N. galajuga*) possess smooth subcaudal scales (Fig. 2). Presently, all other known members of the *N. pelagicus* complex from New Guinea into Oceania possess keeled subcaudals. Keeled subcaudal scales, no or small postmental scales (Postm), and numerous (>30) tubercles in the dorsal tubercle rows (TubRow) differentiate the PNGW sample from all known populations of Australian *N. 'pelagicus'*. These differences suggest that PNGW represent a distinct species and is likely not a member of the Australian clade, so it is excluded from further comparisons.

The preceding sexual comparisons reveal that in all samples except CHIL2, TINA and DUNK2, some mature $\delta\delta$ have precloacal pores. There appears to be a break between MCIL and FLIND with pores regularly >6 in northern populations and usually <3 in the southern ones. The occurrence of some $\delta\delta$ with femoral pores shows a similar geographic break, with FLIND $\delta\delta$ and all samples to the S lacking femoral pores and some $\delta\delta$ in MCIL and other northern samples with femoral pores, although these pores are absent in the VRIL, MAPO and WENL samples. These three samples are small, and pores may be present in a few members of these populations but

were not found because the femoral pores usually occur in less than 50% of the $\delta\delta$.

Scale variation within the total Australian sample is summarised in Table 2 and the variation within and among the local samples in the Appendix 2. From the perspective of either the local samples or the total sample, Suplab, DorsTub, TubHip, ForefL and HindfL have low variability (cv < 15%) and show no geographic trends. Inflab, TubRow, TubHindl, and Palm are moderately variable (cv = 16-25%). Inflab, TubRow, and Palm generally show lower means in the S, but the pattern is not clinal. TubHindl shows two states in Australian *N. 'pelagicus'* (Fig. 3): tubercles on dorsal surface of both thigh and crus (tuberculate thigh); and tubercles on only the dorsal surface of the crus (naked thigh). Both states occur throughout CYP, although the naked-thigh state is absent in most samples N of and including COOKT, occurring at low frequency in the SOMER and FLIND samples and in the single NYMPH specimen. In contrast, from MTCAR southward, the naked-thigh state is common and the higher frequency suggested the segregation of the local samples into tuberculate- and naked-thigh samples (e.g., CHIL1, CHIL2, respectively).

The remaining characters range from borderline variable (Postm, CloaS) to extremely variable PnLab, TubDen, CST, PreclPor, FemPor). Postm shows the same variability in each local sample as in the total sample and suggests no geographic pattern. Throughout the Cape, most individuals typically have two cloacal spurs (CloaS) on each side of the tail base; however, the one-spur state has a higher frequency in northern samples. Cloacal spurs are more often rounded than pointed (CST), although the pointed state is common in MTCAR and TINA. The extension of chin scales between the postmental and the infralabial scales (PnLab) occurs in a single IRON specimen and in a third of the FLIND ones; in all other Australian specimens, the postmentals and

infralabials touch. Most Australian *N. 'pelagicus'* lack enlarged tubercles on the front of the thigh (TubDens) even if the thigh is tuberculate dorsally.

Even though there are no strong geographic patterns in scale variability, many neighbouring samples have one or more scale characters displaying significant differences ($t < 0.05$), excluding comparisons with precloacal and femoral pores because of their dimorphism. The pair TORR-SOMER are significantly different in Postm, TubRow, ForefL and Palm. The pairs SOMER-VRIL and MAPO-VRIL have no differences, but MAPO-NOAL and WEIPA-NOAL differ in TubRow. MAPO-WEIPA differ in Suplab and HindfL. The E central samples display more significant differences between neighbouring sample pairs. WENL-IRON differ in DorsTub, ForefL, HindfL and Palm; WENL-MCIL by Inflab and TubRow; and MCIL-FLIN by Inflab, Postm, TubRow, TubDens, HindfL and Palm. The southern sample-pairs have low and moderate levels of differences. COOKT-MTCAR1 have no differences; COOKT-CAIR differ by Postm, TubRow and Palm; CHIL1-CHIL2 by TubRow, ForefL and Palm; and DUNK1-DUNK2 by TubRow. Within this southern area, the greater frequency of naked-thigh specimens warrants a comparison of the COOKT-LAURA-MTCAR1-CHIL1-DUNK1 sample (tuberculate) with the MTCAR2-CAIR-CHIL2-TINA-DUNK2 sample (naked). Seven characters show significant difference: Postm, DorsTub, TubRow, TubHindl, ForefL, HindfL and Palm (Table 3). The syntypic series of *marmorata* de Vis (= *cheverti* Boulenger) consists of naked-thigh specimens from Fitzroy I. and tuberculate-thigh ones from Endeavour R.; aside from the thigh tuberculation, the two sets of specimens differ only by TubRow and TubHindl. The large distance between COOKT and the E-central samples has a potential for major differences, yet COOKT-FLIN show only Palm differing, but COOKT-MCIL show Suplab, Inflab, Postm, TubRow, TubRow, TubDens, CloaS and CST. Thus, COOKT-MCIL and MCIL-FLIN have a similar level of differences.

Although other paired comparisons are possible, the preceding ones explore the major regional

TABLE 3. Select mensural and scalation characters for southern naked-thigh (NYMPH, MTCAR2, CAIR, CHIL2, TINA, DUNK2) and southern tuberculate-thigh (COOKT, LAURA, MTCAR1, CHIL1, DUNK2) samples of *Nactus pelagicus*. Character name abbreviations as in Table 1.

Mensural Characters						
	SVL	TrunkL	HeadL	NarEye	Interorb	
Tuberculate (mean $\pm$ SD)	43.3 $\pm$ 2.6	17.9 $\pm$ 1.7	11.8 $\pm$ 0.6	3.7 $\pm$ 0.3	3.5 $\pm$ 0.3	
Range (n = 56)	38.4-50.0	14.4-22.3	10.6-13.5	3.1-4.3	2.8-4.2	
Naked (mean $\pm$ SD)	46.3 $\pm$ 4.1	20.0 $\pm$ 1.2	12.3 $\pm$ 1.2	3.9 $\pm$ 0.5	3.3 $\pm$ 0.3	
Range (n = 22)	39.2-57.0	13.2-25.4	10.4-15.6	3.1-5.2	2.8-4.2	
Scalation						
	Postm	DorsTub	TubRow	ForefL	HindfL	Palm
Tuberculate (mean $\pm$ SD)	15.8 $\pm$ 3.9	14.4 $\pm$ 1.1	18.0 $\pm$ 1.7	14.5 $\pm$ 0.9	18.3 $\pm$ 1.1	5.3 $\pm$ 0.9
Range (n = 69)	8-26	11-17	15-21	13-17	15-20	3-8
Naked (mean $\pm$ SD)	12.4 $\pm$ 4.0	13.6 $\pm$ 1.0	21.3 $\pm$ 3.2	13.5 $\pm$ 0.8	17.4 $\pm$ 1.4	4.9 $\pm$ 0.6
Range (n = 32)	2-24	12-16	17-27	12-15	14-20	4-6

ties, and additional ones appear redundant and do not demonstrate any additional variation patterns. Another approach is to examine the distribution of all individuals in multivariate space. Principal components analysis (all scale characters and all samples, including TYPE) examines the level of variation within all (or a select set of) scale characters of all sample localities simultaneously. PCA of the total character set (excluding only Subcaud which is invariant and TubDens which is not applicable to naked-thigh specimens) for the total Australian sample shows TubRow, Postm and PreclPor to have the major influence (PC loadings: -4.9, 1.8, -1.7, respectively) on the first factor or component. Postm and PreclPor are the major ones for the second component, and PreclPor for the third component. The first three components account for 87% of the total variance (50, 21, 16%, respectively). Bivariate scattergraphs of component pairs reveal no segregation of the samples in multivariate space. Similar results (Fig. 4) obtain with a PCA excluding the sexually dimorphic pore characters and TubDens. The sequence of component loading remains the same as in the total character analysis, except ForefL and HindfL replace the pore characters; the first three components account for 92% of the total variance. A varimax rotation of component axes yields some segregation of the northern and southern populations, although significant overlap occurs. The lectotype of *Heteronota marmorata* Macleay lies in the centre of the cluster.

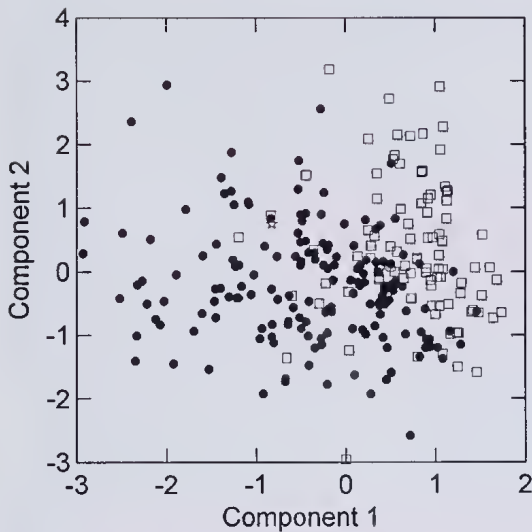


FIG. 4. Distribution of Australian *Nactus* in multivariate space derived from a PCA of scalation (covariance matrix, varimax rotation). The first component reflects mainly the variation of TubRow; the second component Postm and TubRow. ●=individuals of the northern population; □=southern population; ☆=lectotype of *Heteronota marmorata* Macleay (= *N. cheverti*).

Discriminant function analysis (DFA) permits a test of the uniqueness of a priori groups by identifying the character(s) that best segregate the groups and whether each individual is assigned to its a priori group. The subsequent DFA used 12 scalation characters, excluding the sexually dimorphic pore characters, TubDens (absent in naked-thigh specimens), PmLab (nearly invariant), and Subcaud (invariant), occasionally also excluding TubHindl.

DFA of naked- and tuberculate-thighs groups yields strong discrimination based mainly on TubHindl and assigns all naked-thigh individuals to their group and 98% of tuberculate-thigh group members to their group. The four individuals (2%; AMSR16479, 64046, QMJ26237, 36192) misclassified are the specimens with the naked thighs in the northern tuberculate-thigh samples. Reassigning these four individuals to the naked-thigh group and reanalyzing yields 100% correct assignment to both a priori groups; again TubHindl is the character weighed most strongly for discrimination classification.

DFA of the northern samples (TORR, SOMER, VRIL, MAPO, NOAL, WEIPA, HORSE, IRON, WENL, MCIL) and the southern ones (FLIND,

COOKT, MTCAR1 & 2, CAIR, CHIL1 & 2, TINA, DUNK), excluding TubHindl, yields moderate discrimination of northern and southern individuals, 85% and 82% correct a posteriori classification, respectively. The classification functions for each character differ little for the N and S groups and only Inflab, Postm and TubRow group-means (3.0, 2.7; 12.6, 14.8; 25.1, 19.1; respectively) differ by more than 0.3, and only Inflab and CloaS have moderately different weights for the classification functions. Misclassified northern individuals derive from six samples (TORR, SOMER, MAPO, WEIPA, IRON, MCIL) and southern ones from six samples (FLIN, COOKT, CAIR, CHIL2, DUNK2, TYPES [one each from Endeavour R. & Fitzroy I.]). With the exception of the entire CAIR sample ($n = 5$), there is no obvious character or set of characters causing the misclassification. The combination of small Postm and high TubRow in the CAIR individuals appear to produce their incorrect group assignment.

DFA comparison of adjacent regional samples (same sample pairs as for the earlier t tests of scalation means) yields no northern samples in which correct classification is 100%. Among the southern samples, CAIR-COOKT, CHIL1-CHIL2, and DUNK1-DUNK2 have 100% correct group assignment, and this accuracy derives from TubHindl. Considering the possibility of three taxa (northern tuberculate-thigh, southern tuberculate-thigh, and southern naked-thigh [including the two insular naked-thighed individuals from FLIN and NYMPH]), DFA correctly classifies all southern naked-thighs, 94% of the southern tuberculate-thighs, and 85% of the northern sample. All misclassified southern tuberculate-thighs (4 of 66) are assigned to the northern sample. The misclassified northern specimens ($n = 164$) are two to the southern naked-thighs and 23 to the southern tuberculate-thighs. TubHindl is the major discriminator, hence the misclassification of the two SOMER specimens with naked thighs. CST, Palm, and Postm are the next set of characters with the greatest differential weights.

MORPHOMETRY. Sexual variation. Among the six Australian samples (Table 4), TORR and WEIPA show no significant differences ($p < 0.05$) between the meristic characters of ♀♀ and ♂♂. Variance is homogeneous between all samples for all characters. MCIL possesses significant differences between the sexes in only SVL, but variance is unequal between the two sexes. SOMER shows significant differences for only TrunkL and NeckL with ♀♀ having longer

TABLE 4. Select mensural parameters showing sexual dimorphism in some samples of adult Australian *Nactus*. Values are the mean $\pm$ one standard deviation; character abbreviations as in Table 1.

Locality	♀ ♀				
	n	SVL	TrunkL	HeadW	NarOrb
TORR	13	47.8 $\pm$ 3.3	20.2 $\pm$ 1.8	8.7 $\pm$ 0.6	4.0 $\pm$ 0.4
SOMER	11	46.2 $\pm$ 3.8	19.9 $\pm$ 2.0	8.2 $\pm$ 0.9	3.8 $\pm$ 0.4
WEIPA	16	48.0 $\pm$ 3.4	20.5 $\pm$ 2.0	8.9 $\pm$ 0.5	4.2 $\pm$ 0.6
IRON	08	48.4 $\pm$ 3.5	20.1 $\pm$ 1.4	9.7 $\pm$ 1.0	4.1 $\pm$ 0.4
MCIL	08	49.8 $\pm$ 5.6	20.3 $\pm$ 3.2	8.9 $\pm$ 1.0	3.4 $\pm$ 0.4
COOKT	16	45.5 $\pm$ 2.5	18.6 $\pm$ 1.6	8.4 $\pm$ 0.5	3.4 $\pm$ 0.4
Locality	♂ ♂				
	n	SVL	TrunkL	HeadW	NarOrb
TORR	06	45.4 $\pm$ 3.3	18.8 $\pm$ 2.8	8.4 $\pm$ 0.7	3.8 $\pm$ 0.2
SOMER	17	44.7 $\pm$ 4.6	17.7 $\pm$ 2.1	8.2 $\pm$ 0.8	3.7 $\pm$ 0.4
WEIPA	16	47.1 $\pm$ 3.1	20.1 $\pm$ 1.7	8.5 $\pm$ 0.7	3.4 $\pm$ 0.4
IRON	12	44.8 $\pm$ 3.0	18.3 $\pm$ 1.1	8.1 $\pm$ 0.8	3.7 $\pm$ 0.4
MCIL	18	46.3 $\pm$ 2.0	19.0 $\pm$ 1.4	8.7 $\pm$ 0.7	3.6 $\pm$ 0.4
COOKT	17	42.1 $\pm$ 2.0	17.2 $\pm$ 1.5	7.9 $\pm$ 0.4	3.7 $\pm$ 0.3

trunks (mean = 19.6mm) and shorter necks (mean = 7.0mm) than ♂ ♂ (mean = 17.7, 7.6mm, respectively). IRON and COOKT possess similar suites of sexually dimorphic characters SVL, TrunkL, HeadL, HeadW, and Interorb; individually IRON also has ♀ ♀ and ♂ ♂ significantly different in HeadH and NarOrb and COOKT in EyeD. In both IRON and COOKT, ♀ ♀ (mean = 45.5, 48.5mm SVL) are larger than ♂ ♂ (mean = 42.1, 44.8mm SVL).

The New Guinea sample (PNGW) shows no significant differences between the mensural means of the ♀ ♀ and ♂ ♂. Variance is homogeneous between the sexes for all characters except NeckL ($p = 0.03$). Because the PNGW sample lacks the unique subcaudal feature of all Australian *Nactus* and likely represent a different clade, it is excluded from further comparison.

IRON and COOKT have a similar suite of sexual dimorphic mensural traits, thus geographic variation among the Australian samples is examined only in adult specimens and separately by sex.

Geographic variation. The Australian samples show no pattern of size variation. Mean SVLs vary from 44.9 to 52.0mm in ♀ ♀ and from 40.4 to 48.6mm in ♂ ♂, although the larger samples ($n > 5$) have narrower ranges of means (44.9-49.8mm ♀ ♀, 44.5-47.1mm ♂ ♂). The largest ♀ (57.0mm SVL) is from CAIR and the largest ♂ (57.6mm) is from SOMER. The small samples from many localities offer no confidence to either the presence or absence of any geographic size differences; however, the similarities of the mean SVLs among the larger samples and the low to moderate coefficients of variation ($cv = 4$ -10%)

for all samples suggest a general size uniformity throughout the CYP populations. This uniformity is also indicated by moderate (7.5%) coefficients (cv) for both the total ♀ (mean = 47.3 $\pm$ 3.5mm, $n = 111$) and the total ♂ (mean = 44.9 $\pm$ 3.4mm, $n = 132$) samples. This uniformity and consistency of means and standard deviations exist for all other mensural traits. Notably, the combined samples emphasize the presence of sexual dimorphism in all mensural traits ($p < 0.02$), except NeckL ($p = 0.20$).

Although the univariate comparisons of mensural traits reveal no regional differentiation, the tuberculate-thigh and naked-thigh

conditions suggest populational differentiation, and as in scalation, a MTCAR2-CAIR-CHIL2-TINA-DUNK2 sample represents the naked-thigh population. A comparison of this sample to a sample of all other sample localities shows only InterOrb differing in size (both ♀ ♀ and ♂ ♂) between the two combined samples. Multivariate analyses (PCA) of transformed variables, separately for adult ♀ ♀ and ♂ ♂, also demonstrates a size uniformity within each sex between the two samples. ♂ ♂ and ♀ ♀ share the same major variables (HeadL, SVL, HeadW) and the same loading ordering of these three variables on the first component; in both sexes, HeadL accounts for 53% of the total variance. These three variables account for 72.5% (♂ ♂) and 74.8% (♀ ♀) of the total variance. The first component is strongly size associated. No bivariate plot of any paired combination of the five components yields any striking outliers, and none of the nearby outliers consistently represents the same individuals. Type specimens were included in the analyses, and all, including the lectotype (AMSR42733) of *Heteronota marmorata*, lie within the PC centroids. Thus, no morphometric differentiation of naked- and tuberculate-thigh populations is evident.

DISCUSSION

LOCAL AND REGIONAL VARIATION IN CHARACTERS. A striking feature of the Australian *Nactus* is the smooth subcaudal scales (Fig. 2). This feature is unique in Pacific *Nactus*, occurring only in *N. galgajuga* and the Australian *N. 'pelagicus'*. The Mascarene *N. coindemirensis* and *N. serpensinsula* also possess smooth

subcaudals. At this time, it cannot be determined whether this character state is primitive, shared-derived, or of multiple independent origins. Nevertheless, its occurrence does suggest a single ancestor for all Australian *Nactus*.

Greer (1989) suggested that adults from northern populations were larger than adults of southern ones (region of Princess Charlotte Bay being the dividing line). A preliminary analysis of small samples from both N and S of the bay confirmed this difference. The analyses here of major samples and the entire Australian sample, however, find no significant differences in mean body size between northern and southern samples, although the single major southern sample (COOKT) has the smallest mean SVL for both adult ♀♀ and ♂♂ (Table 4). In both northern and southern samples, ♀♀ regularly average larger than ♂♂, often significantly so, but these differences are not great, ranging 2-3mm. The other mensural characters show similar sexual dimorphisms that are statistically significant in the larger samples but slight in actual measurements and invisible to the human eye. None of the analyses of the mensural data reveals a pattern of regional differences and offers no evidence of genetic differentiation among the Australian populations. Because the differences are slight, are not evident in all mensural characters, and are not displayed in the same suites of characters in different samples, they are as likely to arise from measurement error and small sample sizes rather than being a reflection of microdifferentiation.

Greer (1989) also observed differences in the number of precloacal pores in the northern (5-11) and southern (0-3) populations. His observation holds with the addition of a qualifying statement: if pores are present in adult ♂♂. Precloacal pores do not occur in all adult Australian ♂♂; when present, northern ♂♂ have 4-11 and southern ones 1-5. With the exception of two northern samples (TORR, IRON), PrecIPor do not occur in adult ♀♀. The frequency of PrecIPor occurrence in ♂♂ is low in some northern samples (e.g., 30% MAPO) and can be strikingly different between adjacent sample localities (e.g., 30% MAPO vs 100% WIEPA, 83% IRON vs 50% WENL). Because only functional pores were recorded, their absence in some individuals may be due to individuals' larger than minimum adult size yet not sexually mature. Nonetheless, the absence of pores occurs in larger specimens as well as small ones. Another possibility is a cyclic nature to pore secretion, although one would as-

sume that nonperforated pores would be visible in the pore scales, but such a condition was not commonly observed. These observations and the erratic occurrence of femoral pores in ♂♂ with PrecIPor and even a few ♀♀ with PrecIPor suggest that precloacal pores are truly absent in some adult ♂♂. Only northern samples and not all of them have some ♂♂ with FemPor.

Scalation, aside from the precloacal/femoral pores, suggests no sexual dimorphism but shows high interpopulational variation, although quantitative differences among samples are slight. The most striking character difference is the presence or absence of tubercles (large keeled scales) on the thigh. Naked-thigh individuals are rare in the samples from the northern half of CYP, with only three specimens (2 SOMER & 1 FLIN) or approximately 1% of the total northern sample. In contrast, naked-thigh individuals comprise nearly half of the southern sample (NYMPH and southward). Although these morphs might represent two distinct populations in the S, no other aspect of scalation supports such an interpretation (see Appendix 2).

Scalation in general does not offer a strong argument for even the N-S segregation of populations. Often the variation between adjacent sample localities is as great or greater than between more distant ones. Visual inspection of the sample means for the samples (Appendix 2) suggests somewhat larger postmentals (Postm), higher number of dorsal tubercle rows (TubRow), more often one rather than two cloacal spurs (CloacS), and more palm scales (Palm), but the differences are weak and not consistent within either the northern or the southern sample.

Multivariate analyses also demonstrate weak differentiation among samples. PCA reveals no discrete clustering for any sample. It identifies Postm, TubRow, and PrecIPor as the major contributors to the variation among and within samples. DFA identifies TubHindI as the major discriminator for classifying a priori groups. When this character is removed, Inflab (infralabials), Postm, and TubRow become the major discriminators, but misclassification increases to 15-20% in contrast to the 0-5% when TubHindI is included in the analysis.

SPECIATION. The primary question is whether the observed morphological differentiation resulted from speciation of and within Australian *Nactus* 'pelagicus'. The uniqueness and uniformity of the subcaudal scales among Australian populations strongly indicates speciation.

Furthermore, Moritz's (1987) karyotype data of a single Australian population ($2N = 38$) are strikingly different from any other '*pelagicus*' population ($2N = 28, 35$ or 36). Donnellan & Moritz (1995) show that two Australian populations are more similar to one another in allozymes than to any New Guinean or Oceania populations. All these data support the recognition of the Australian populations as distinct species.

The second aspect of the question is whether speciation has occurred among the Australian populations. Although I am convinced that the regional differentiation reflects two, perhaps even three species, the nature of the morphological variation does not permit an unequivocal decision. I advocate the recognition of two species, a northern and a southern one, divided at the head of Princess Charlotte Bay as suggested by Greer (1989). The present samples cannot address whether these two species are allopatric, parapatric, or of limited sympatry. The number of precloacal pores and the presence or absence of femoral pores in adult ♂♂ are the only two characters that provide decisive evidence of distinctiveness. Inflab, Postm, CloacS, HindfL, and Palm show some tendencies to differ between the N and S groups, but the ranges of means of the N and S samples overlap and in each listed character, either a northern or a southern sample has a mean at the minimum or maximum of the other group's range.

The early recognition of naked-thigh individuals and their concentration in southern populations suggested to me that two species, naked-thigh and tuberculate-thigh, existed rather than the N-S speciation as proposed above. Perhaps the southern naked-thigh individuals do represent a separate species. While that concept is tempting, the available museum specimens suggest the co-occurrence of the two morphs, and I lack field experience with them to suggest that they are not microsympatric as well. Further, the low frequency occurrence of the naked-thigh condition in the northern samples negates the immediate recognition of the southern naked-thigh populations as distinct. Whether this trait differentiates species or represents a single genic polymorphism requires microhabitat observations and electrophoretic or DNA analysis.

Because of the equivocal nature of the northern and southern species, biogeographic comments are inappropriate. I note only that the two species' distributions match the CYP and Atheron areas of endemism found in other Australian plants and animals (Cracraft, 1991). Also the variation among neighbouring samples suggest that disper-



FIG. 5. Geographic distribution of *Nactus cheverti* (□) *Nactus eboracensis* (●), and *Nactus* sp-New Guinea (◇) in CYP and the Torres Strait Is; Δ = the restricted type-locality of *Heteronota marmorata* Macleay (= *N. cheverti*).

sal is low and that each population is experiencing and adapting to local selective pressures.

A noteworthy distributional feature is the occurrence of the New Guinean *Nactus* in the Torres Strait Is nearly to CYP (Fig. 5). They are potentially sympatric on only one island, Mount Ernest I. I have confirmed a single specimen of each species from this island. *N. eboracensis*' most northerly record is from Yam I., and the New Guinea *Nactus* occurs as far S as Hammond, Booby, Friday and Prince of Wales islands. No other lizard shows this distributional pattern, although *Gehyra baliola*, a New Guinean species, occurs in the NE Torres Strait islands (Darnley, Murray) and is replaced in the southern islands by *G. dubia* and an undescribed species (King et al., 1989).

TAXONOMIC RÉSUMÉ AND CONCLUSIONS

Macleay (1878) was the first to recognize the distinctiveness of the Australian *Nactus*. Although his descriptions do not differentiate among the two Australian species of the *N. pelagicus* complex, he named specimens from Fitzroy I. and the Endeavour R. as *Heteronota marmorata* and two specimens from CY (presumably the telegraphic station or cape of that name at the tip of the peninsula) as *Heteronota eboracensis*. In his catalogue, Boulenger (1885) assigned *Heteronota marmorata* to the genus *Gymnodactylus*. His action made *marmorata* a secondary homonym and hence no longer available as a specific name for the Endeavour-Fitzroy populations; thus, he proposed the replacement name *cheverti* for *marmorata* Macleay. (I.C.Z.N. Article 59b – a junior secondary homonym replaced before 1961 is permanently invalid.) Boulenger (1885) also listed *eboracensis* as a *Heteronota*, noting his uncertainty of this assignment.

Macleay's and Boulenger's names remained unused until 1913 when F. Werner used *Gymnodactylus Cheverti* for a specimen he had acquired from Brisbane. Zietz (1920) referred to both *G. cheverti* and *H. eboracensis* for Fitzroy I. and northern Queensland specimens, respectively, in his catalogue of Australian lizards. The names again disappeared from the herpetological literature for over 60 years until Wells & Wellington (1984) resurrected *Nactus eboracensis* in their checklist, providing no analysis or explanation. Owing to the absence of justifications for their nomenclatural action, their usage was not adopted by the herpetological community.

None of the preceding usages or actions affects the availability of *Gymnodactylus cheverti* Boulenger and *Heteronota eboracensis* Macleay, hence these names can be assigned to the southern and northern species, respectively. The type locality of *H. marmorata* is precise and of unquestionable provenance, i.e., Endeavour R. and Fitzroy I., both of which are within the range of the southern species. Further, all syntypes are recognisably from the southern population and are so classified by discriminant function analysis. Kluge (1963) selected an adult syntype from Fitzroy I. as the lectotype, thus functionally restricting the type locality to this island. Under my two species interpretation, this lectotype selection has no effect on name assignment to the southern populations; however, if the naked-thigh *Nactus* is a separate species, then *cheverti* Boulenger becomes the name for the naked-thigh species and the southern tuberculate-thigh species has no available name.

The situation for the northern species is not as straightforward because the lectotype and paralectotype of *H. eboracensis* have deteriorated and are barely recognisable as specimens of *Nactus*. Thus, their condition excluded them from the character analyses. In addition, the type locality of *H. eboracensis* is given only as 'Cape York', which is insufficient to determine unequivocally whether the name applies to the entire Peninsula or the telegraphic station/cape at the tip of the Peninsula. I accept the latter interpretation, because Macleay used precise place names for his other taxa. Furthermore to ensure nomenclatural stability, I restrict the type locality of *Heteronota eboracensis* Macleay to the former telegraphic station of CYP (10°43'S 142°28'E).

In conclusion, the Australian species of the *Nactus pelagicus* complex are:

Nactus cheverti (Boulenger)

Heteronota (sic) *marmorata* Macleay, 1878: 100. Type-locality, 'from Fitzroy Island and Endeavour River'. Kluge (1963) designated a lectotype (Macleay Museum R632, now AMSR42733), thereby restricting the type-locality to Fitzroy I. *Gymnodactylus cheverti* Boulenger, 1885: 41. Nomen novum for *Heteronota marmorata*.

DEFINITION. A bisexual *Nactus* ranging in adult size from 38.4–57.0mm SVL (♀, 41.6–57.0mm; ♂♂, 38.4–48.4mm). Head scales small and granular except for enlarged scales bordering nares and mouth; 3–4, usually 3, supralabials in front of orbit; mental scale pentagonal and extending posteriorly between pair of small to moderate-sized postmentals; postmental almost always in contact with first infralabial. Dorsally nape, neck, and trunk covered by small, multi-keeled, cone-shaped scales and longitudinal rows of large, multi-keeled, cone-shaped tubercles, 11–17, commonly 14–15, rows at midbody, 15–27 usually 20 or fewer, tubercles in the parasagittal row between the axilla and inguen, and 6–10, usually 8 rows across hips; ventrally small, flattened, uncarinate scales from throat to vent. Thigh and crus with moderate number of enlarged keeled tubercles among small cone-shape scales; thighs lack tubercles in 30–50% of individuals. Tail round in cross-section with moderate-sized, slightly overlapping, keeled scales dorsally; scales cycloid and smooth ventrally. When present, 1–5 usually 3 or fewer precloacal pores in adult ♂♂; no precloacal pores in adult ♀♀ and no femoral pores in ♂♂. ♀♀ and ♂♂ usually with 2, occasionally 1 or 3, cloacal spurs on each side of tail base. Subdigital lamellae

enlarged, undivided, and smooth; 12-17, usually 14 or fewer, lamellae on fourth finger, 14-20, usually 18, or fewer on fourth toe. Karyotype, $2N = 35$ (Moritz, 1987).

DISTRIBUTION. Southern half of CYP from Flinders I. Group and Melville Peninsula southward.

Nactus eboracensis (Macleay)

Heteronota eboracensis Macleay, 1878: 101. Type-locality, 'Cape York'. Kluge (1963) designated a lectotype (Macleay Museum R975, now AMSR31940); the type-locality is restricted to CY (former telegraphic station) ($10^{\circ}43'S$ $142^{\circ}28'E$).

DEFINITION. A bisexual *Nactus* ranging in adult size from 37.9-57.6mm SVL ($\varnothing$, 41.1-56.7 mm; $\sigma\sigma$, 37.9-57. mm). Head scales small and granular except for enlarged scales bordering nares and mouth; 3-4, usually 3, supralabials in front of orbit; mental scale pentagonal and extending posteriorly between pair of small to moderate-sized postmentals; postmental almost always in contact with first infralabial. Dorsally nape, neck, and trunk covered by small, multikeeled, cone-shaped scales and longitudinal rows of large, multikeeled, cone-shaped tubercles, 12-18, commonly 13-14 rows at midbody, 15-37, usually more than 22, tubercles in the parasagittal row between the axilla and inguen, and 4-12, usually 8, rows across hips; ventrally small, flattened, unicarinate scales from throat to vent. Thigh and crus with moderate number of enlarged keeled tubercles among small cone-shape scales; thighs rarely lacking tubercles. Tail round in cross-section with moderate-sized, slightly overlapping, keeled scales dorsally; scales cycloid and smooth ventrally. When present, 4-11, usually 6 or more, precloacal pores in adult $\sigma\sigma$; occasionally 1-2 precloacal pores in adult $\varnothing\varnothing$, and rarely 1-3 femoral pores in $\sigma\sigma$, sometimes on one side only. $\varnothing\varnothing$ and $\sigma\sigma$ usually with 2, occasionally 3, cloacal spurs on each side of tail base. Subdigital lamellae enlarged, undivided, and smooth; 11-18, usually 15 or fewer, lamellae on fourth finger, 15-23, usually 18 or fewer, on fourth toe. Karyotype, unknown.

DISTRIBUTION. Torres Strait Is of Great Woody, Horn, Mount Ernest, Thursday, Wednesday, Yam, York, and the northern half of CYP from W side of Princess Charlotte Bay northward.

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APPENDIX 1

SPECIMENS EXAMINED. The samples are divided into two sets. The first set includes the specimens used in the statistical analyses. The capitalised abbreviations of localities are used in the text; sample size in parentheses, sequentially adult ♀♀, adult ♂♂, juveniles. The second set contains specimens examined to confirm the specific identity of each individual. Both sets are ordered geographically N to S, E to W. Museum abbreviations follow Leviton et al., 1985.

TYPES.

- Heteronota eboracensis* Macleay: AMSR29951 (lectotype), 29952.
- Heteronota marmorata* Macleay = *Gymnodactylus cheverti* Boulenger: Endeavour R. AMSR31937-43; Fitzroy I. AMSR42733 (lectotype), 42734-35.
- PNGW southern Fly R. delta, Western Province, PNG, 8°05'S 142°50'-56'E (13, 11, 3) *Nactus* sp.: MCZ123212 (Adiba); MCZ124299 (Boze); MCZ124313 (Mememorac); MCZ121165 (Wipim); MCZ131132-33, 141115, 141117-19, 141122-25, 141127-30 (Emeti); USNM195757, 325059-66 (Emeti).
- TORR Torres Strait Is, 10°15'-37'S 142°13'-28'E (13, 6, 1) *N. eboracensis*: MCZ124298, QMJ25658-59, 25695, 25821 (Hom I.); MCZ140953 (Mt Ernest I.); AMSR42241-42, 42379, 44241, 58959, MCZ137658-60, QMJ58151 (Thursday I.); AMSR61982, 61985 (Wednesday I.); QMJ52378, 52381, 52383 (Yam I.).
- SOMER tip of CYP, Somerset area, 10°50'-11°45'S 142°10'-35'E (11, 18, 0) *N. eboracensis*: AMSR16479, 38515-17, 38520, 38522, 56040, 56043, 56045-46, 56048, 56059, 56215, 56287, QMJ24670-71, 26237, 42785, 42789, 45587, 45589-90, 54018-19, 54023, 54029, 54034, 54037, 54102.
- VRIL Vrilya Pt, 11°13'S 142°07'E (1, 4, 0) *N. eboracensis*: AMSR99713-14, 99727, 99734, 99764.
- MAPO Mapoon Mission, 11°58'-59'S 141°53'E (8, 10, 0) *N. eboracensis*: AMSR99700-02, 99704, 99989-91, 105060, 105110, 105129-35, 105142, 126033.
- NOAL North Alice R. crossing, 12°04'S 142°21'E (2, 4, 1) *N. eboracensis*: AMSR99766, 99927, 99934-38.
- WEIPA Weipa, 12°44'S 141°52'E (16, 16, 0) *N. eboracensis*: AMSR22134, 22140-41, 62110, 62112-14, 62122, 62129, 82218, 82220-21, 82369, 82393-95, 82398-99, 105032-33, 105089-95, QMJ25768-69, 39767, 39789 39791.
- IRON Iron Ra. area, 12°37'-54'S 143°00'-24'E (8, 12, 3) *N. eboracensis*: AMSR38524, 38526, 69938-40, 81923, 94104-06, 94144, 94154-55, 94171, 94508, 94518, QMJ28043, 32010-12, 34377-79, 43649.
- WENL Wenlock R. crossing, 13°06'S 142°56'E (10, 2, 0) *N. eboracensis*: AMSR94021-24, 94026, 105345-50, QMJ26687.
- HORSE Horse Trailer W.H., 13°25'S 142°02'E (0, 1, 0) *N. eboracensis*: QMJ58211.
- MCIL Mcllwraith Ra., 12°43'-13°58'S 143°11'-32'E (5, 18, 0) *N. eboracensis*: AMSR16261, 16268-69, 16298, 16356, 16358, 16474, 16704-05, 16712, QMJ34466-68, 34526, 34537, 38103, 38105, 38143, 38308, 38460-61, 38464.
- FLIN Flinder I Group, 14°06'-13'S 144°15'-20'E (4, 4, 0) *N. cheverti*: QMJ36165, 36192, 36194, 36207-09, 36217-18.
- NYMPH Nymph I., 14°39'S 145°15'S (0, 1, 0) *N. cheverti*: AMSR64046.
- COOKT Cooktown area, 15°24'-28'S 145°06'-15'E (16, 17, 1) *N. cheverti*: AMSR26675, 26679, 26687, 26738-39, 31937, 31940, 31942, 69934-35, 69937, 85962, 85965, 126031-32, 126034-38, 126040, 126046-47, MCZ136021, 136023, 136028, 136030-31, 136155, 136161, 136166, QMJ25206, UMMZ131494-95.
- LAURA Laura, 15°40'S 144°31'E (1, 0, 0) *N. cheverti*: QMJ38009.
- MTCAR1 Mt Carbine area, 16°19'-41'S 145°01'-20'E (0, 6, 2) *N. cheverti*: AMSR63904-07, 63910-11, 63913 (Windsor Tableland); QMJ40640 (Mt Carbine).
- MTCAR2 Mt Carbine area, 16°19'-41'S 145°01'-20'E (1, 0, 1) *N. cheverti*: AMSR38506 (Mt Carbine); QMJ19332 (Mt Molloy).
- CAIR Cairns area, 16°55'S 145°46'E (2, 1, 2) *N. cheverti*: AMSR42734, 85949, 94523, 119680, MCZ118879.
- CHIL1 Chillagoe area, 17°09'-19'S 144°30'-145°13'E (0, 3, 3) *N. cheverti*: AMSR85961-65, QMJ47102.
- CHIL2 Chillagoe area, 16°19'S-17°53'S 144°30'-35'E (4, 3, 6) *N. cheverti*: AMSR85950-55, 86738, 86904, 142590, 14598, 143208, QMJ18038, 31234.
- TINA Tinaroo, 17°10'S 145°33'E (1, 2, 1) *N. cheverti*: AMSR85956-57, QMJ11801-02.
- DUNK1 Dunk I. & adjacent coast, 17°20'-57'S 146°01'-10'E (0, 2, 3) *N. cheverti*: AMR86734 (Bingil Bay); QMJ1908-09 (Dunk II.); QMJ30858 (Innisfall); QMJ55125 (Tully).
- DUNK2 Dunk I. & adjacent coast, 17°10'-50'S 145°15'-146°09'E (3, 1, 0) *N. cheverti*: AMSR 51534 (Russell I.); QMJ52982 (Watsonville); QMJ60832, 61112 (Hann's Tableland).
- UNKNOWN LOCALITIES CYP (1, 1, 0) *N. eboracensis*: MCZ 35135, UMMZ 35135.

Specimens examined to determine specific identity but not for statistical analyses.

Nactus sp New Guinea

TORRES STRAIT IS. Darnley: AMSR42624; Murray: AMSR4515, 42555, 42567-69, 42587-88, 44230, 44272, 45070, 45903-04, 45909-10, 45957-59, 46099, 46135-38, QMJ52384-89; Daur: AMSR45080-87; Badu (Mulgrave) AMSR58975-76, 59068, 59118; Moa (Banks): AMSR46694-95, 46697-706, 46794-97, 46886-89, 46891-95, 46897-900, 46968, 48584; Mount Ernest (Nagir, Nagheer): AMSR4516; Hammond: AMSR42268-69, 42309-15, 44243-44, 47050-58, 47354, 47356; Booby: AMSR36578, 49918, QMJ26003, 26005-007, 27360; Friday: AMSR38527-28, 48941, 48943, 48998-9000; Prince of Wales: AMSR46192-96, 46504-11, 46617-21, 48839-43, 48900-14, 55934-36, 59175, 59178, 59184.

Nactus eboracensis Macleay

TORRES STRAIT IS. Yam: AMSR42375, 42382, 423405-15, 61667, 61743-44, 61747-52, 61825-26, 61870-71, 62469, QMJ52380-83; York (Yorkc): AMSR44246-48, 44346-60, 44363-67; Wednesday: AMSR561968, 61981-85; Thursday: AMSR42241-43, 42322, 44241, 58959, QMJ52378-79; Horn: AMSR48426, 59149-52, 61885-86, 61888, 61918-24, QMJ25657, 25821; Great Woody: AMSR62010.

CAPE YORK. AMSR16261, 16268-69, 16298, 16337, 16339, 16356, 16358, 16474, 16479, 16704-05, 36822, 38507, 38512, 38515-17, 38520, 38522, 38524, 51558, 62117, 62120-21, 62133, 62135, 62137, 86946, 105186, 105314, 38508, 38513-14, 38518, 51559-60, 56746, 62111, 62116, 62118, 62123-24, 62128, 62132, 62136, 62138, 62199-200, QMJ23461, 23479, 23498-99, 23517-18, 24619, 24646, 24650-51, 24670-71, 25657-59, 25695, 25767-69, 25775, 25821, 26223, 26237, 26687, 27155, 28043, 28048, 32010-12, 23257, 34378-79, 34466-68, 34528-29, 34531, 34762, 35377, 34530, 34536, 38099-100, 38102, 38104, 38172, 38276-77, 38199-200, 38280, 38307, 38309, 38314, 38350, 38407, 38409, 38461, 38463, 39753, 39762, 39791, 42789, 43649, 43659, 45586, 45588, 54018-19, 54023, 54029, 54034, 54037, 54084, 54102, 57750, 57799-801, 58151, 58523, 58631-32, 58633.

Nactus cheverti Boulenger

CAPE YORK. AMSR26675-76, 26679, 26683, 26685, 26687, 26732-35, 26738-42, 37203, 38506, 51509-10, 51516-17, 51520, 51526, 51531, 51534, 63908-09, 63914, 64046, 64052, 85949, 85960, 86733, 86735, QMJ11140, 17524-25, 17805, 17819, 25205-06, 25290-91, 25309, 27138, 27257, 36165, 36202-203, 36207, 26209, 30858, 31713, 36192-94, 36217, 36755-56, 45933, 47593, 48087, 51122-25, 53124, 53126, 53137, 53147, 53154.

Nactus galgajuga Ingram

BLACK MTN. QMJ29474 (holotype), AMSR70110 (paratype), (non-types QMJ52973, 61070-72, 61095-96).

APPENDIX 2

Summary of the mean values for the scale characters of the Australian samples of the *Nactus pelagicus* complex. Sample abbreviations are defined in Appendix 1 and character abbreviations in Table 1 and the Materials & Methods section.

	n	Suplab	Inflab	Postm	Dors-Tub	Tub-Row	Tub-Hip	Tub-Hindl	Tub-Dens	CloacS	CST	Precl-Por	Fem-Por	Forefl	Hindfl	Palm
TORR	20	3.3	3.1	12.1	14.0	22.8	8.2	2.0	0.0	1.4	.05	2.0	0.0	13.8	17.4	5.0
SOMER	28	3.2	2.9	14.3	14.1	26.1	8.0	2.0	0.1	1.7	0.2	4.0	0.0	14.3	17.0	5.7
VRIL	04	3.8	2.0	13.0	14.0	28.5	8.0	2.0	0.0	1.0	0.0	0.2	0.0	14.2	17.5	5.5
MAPO	18	3.4	3.1	13.3	13.8	25.2	7.9	2.0	0.1	1.7	0.1	1.3	0.0	14.1	17.0	5.6
NOAL	07	3.3	3.1	12.6	14.0	32.0	7.9	2.0	0.0	1.3	0.0	3.5	1.7	14.0	18.3	5.1
WEIPA	32	3.1	3.0	11.4	14.1	26.9	7.9	2.0	0.1	1.5	0.0	3.7	1.3	14.5	18.8	5.5
IRON	23	3.1	2.8	11.9	15.0	24.2	8.3	2.0	0.3	1.8	0.1	3.8	0.7	14.0	18.1	5.0
WENL	12	3.3	3.0	12.2	13.8	26.7	8.0	2.0	0.0	1.5	0.0	0.0	0.0	14.0	19.4	5.7
HORSE	01	4.0	3.0	10.0	13.0	30.0	8.0	2.0	0.0	2.0	0.0	5.0	0.0	14.0	18.0	7.0
MCIL	23	3.6	3.4	12.8	14.1	21.1	7.7	2.0	0.5	1.4	0.0	4.7	0.3	14.0	19.2	5.7
FLIN	09	3.4	2.0	15.6	14.0	17.3	7.8	1.0	0.1	1.8	0.0	0.2	0.0	14.0	18.1	4.0
NYMPH	01	3.0	2.0	14.1	15.0	19.0	8.0	1.0	-	2.0	0.0	-	0.0	15.0	17.0	5.0
COOKT	34	3.2	2.0	17.0	14.4	17.6	7.9	2.0	0.1	1.8	0.3	0.5	0.0	14.7	18.6	5.7
LAURA	01	4.0	4.0	14.0	14.0	19.0	8.0	2.0	0.0	2.0	0.0	0.0	0.0	14.0	19.0	4.0
MICARI	08	3.1	2.9	14.5	14.6	18.6	8.3	2.0	0.2	1.5	0.5	1.0	0.0	14.4	17.5	5.1
MICAR2	02	3.0	3.0	13.0	13.0	18.0	8.0	1.0	-	2.0	0.5	0.0	0.0	13.5	17.0	5.0
CAIR	05	3.2	2.0	08.4	13.8	25.6	8.0	1.0	-	1.0	0.0	1.0	0.0	14.0	18.4	4.4
CHIL1	06	3.0	2.5	13.3	14.2	17.8	8.0	2.0	0.3	1.5	0.2	0.2	0.0	14.0	18.0	5.3
CHIL2	12	3.2	2.7	12.6	13.7	20.2	8.0	1.0	-	1.7	0.2	0.0	0.0	14.2	17.4	4.5
TINA	04	3.0	2.8	14.5	13.8	18.5	8.0	1.0	-	2.0	0.5	0.0	0.0	12.5	16.0	4.8
DUNK1	05	3.0	2.4	15.2	15.2	20.0	8.0	2.0	0.2	2.0	0.0	0.4	0.0	13.8	17.0	4.4
DUNK2	04	3.2	2.8	14.5	13.2	23.8	8.0	1.0	-	2.0	0.0	0.0	0.0	14.0	17.5	5.2